

HABITAT SPECIFICITY AMONG GROUND SQUIRREL POPULATIONS AT MULTIPLE
SPATIAL SCALES

by

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Abstract

The arctic ground squirrel (*Urocitellus parryii*; AGS) comprised 17% of the herbivore biomass in the Yukon boreal forest during the summer months from 1987 to 1996 and accounted for 23% of the energy flow at the herbivore level. By 2000 these ground squirrel populations had collapsed to nearly zero and today they comprise ~1% of the herbivore biomass in this zone. Most forest populations (~95%) are extirpated, whereas only 65% of low-elevation meadow populations are extirpated. AGS remain abundant in alpine (93% occupancy) and in human altered habitats (97% occupancy).

During spring, postpartum females in forests weighed less and were in poorer condition than females in meadows. However, by onset of hibernation, forest squirrels had reached parity with meadow squirrels in mass and condition. For squirrels in formerly occupied boreal forests a) poor spring body condition likely decreased reproductive success, and b) achieving compensatory growth, via increased foraging, may result in higher predation risk. These costs likely contributed to the recent local extinctions of AGS in boreal forest habitat.

Population densities of AGS and snowshoe hares were estimated over a 25-year period encompassing two snowshoe hare cycles. A hyperbolic curve best describes the per capita rate of increase of ground squirrels relative to their population size, with a single stable equilibrium and a lower critical threshold below which populations drift to extinction. The crossing of this unstable boundary resulted in the subsequent uncoupling of ground squirrel and hare abundance following their mutual declines in 1998. Sustained top-down control of AGS, via a Type II predator response, probably led to their local extinction.

Fine scale habitat features of 138 AGS colonies were measured over a 25,000 km² region of the southern Yukon, 2013-2015. Logistic regression models were constructed to determine which

food, soil, and visibility characteristics best explain colony persistence. Habitat characteristics associated with food, predation risk, and overwinter survival jointly influence the distribution of colony extinctions over large spatial scales. Evidence for multi-factor control of the distribution of this important northern herbivore at the southern portion of its range indicate that numerical responses to environmental change will not be uniform.

Preface

Publications and presentations derived from thesis chapters are described below.

Chapter 2 - Werner, J.R., Donker, S.A., Krebs, C.J., Sheriff, M.J., and Boonstra, R. 2015. Arctic Ground Squirrel Population Collapse in the Boreal Forests of the Southern Yukon. *Wildlife Research*. 42: 176-184. doi: 10.1071/WR14240.

A portion of this chapter was presented as a conference paper: Krebs, C.J., Werner, J.R., and Boonstra, R. 2014. Collapse of Arctic Ground Squirrel Populations in the Yukon Boreal Forest. The 5th International Conference on Rodent Biology and Management. 25-29 August 2014. Zhengzhou, Henan Province, China. Invited paper. doi: 10.13140/RG.2.1.4343.7042j.

Data from this chapter was also presented as a conference paper: Werner, J.R., and Krebs, C.J. 2014. Population recovery under rapid environmental change: lessons from experimental reintroductions. AINA Kluane Lake Research Station Conference proceedings. June 29-30, 2014. Invited poster presentation.

Chapter 3 - Werner, J.R., Krebs, C.J., Donker, S.A., and Sheriff, M.J. 2015. Forest or meadow: the consequences of habitat on female arctic ground squirrel condition. *Canadian Journal of Zoology*. 93: 791–797. doi: 10.1139/cjz-2015-0100.

Chapter 4 - Werner, J.R., Gillis, E.A., Boonstra, R. & Krebs, C.J. 2016. You can hide but you can't run: indirect effects, predator responses and the decline of Arctic ground squirrels in boreal forests of the southwest Yukon. PeerJ 4:e2303 doi: 10.7717/peerj.2303.

An early version of this chapter was presented as a conference paper: Werner, J.R., Gillis, E.A., Boonstra, R. 2016. How apparent competition and predator responses led to the decline of Arctic ground squirrels in the boreal forests of the southwest Yukon. Predator Prey Dynamics: From Theory to Management. Columbia Mountains Institute of Applied Ecology. Revelstoke, British Columbia, Canada. April 5-7, 2016. doi: 10.7287/peerj.preprints.1923v1.

Chapter 5 – an abbreviated version has been submitted to an ecological journal, and is presently under review.

The following published article draws upon various data reported in chapter 2 through 4:

Werner, J.R. 2015. Factors Governing the Distribution and Abundance of Arctic Ground Squirrels. Arctic. 68(4): 521-526. doi: 10.14430/arctic4537.

Except for some long-term monitoring data reported in chapter 3 (1973-present; collected by Charles Krebs and colleagues) and 4 (mass data collected by S. Donker & J. Werner), Jeff Werner designed and conducted all data collection. Jeff Werner conducted the analyses and wrote the manuscripts for all content in this thesis.

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Chapter 1: Introduction

Ground-dwelling sciurid species are a particularly tractable group for examining the influences of external factors on the direction and rate of population change. In this thesis I investigate the various roles that habitat and predators may now play in determining the abundance and spatial arrangement of populations of arctic ground squirrels (*Urocitellus parryii*; hereafter AGS) throughout the southern Yukon, Canada.

Why study arctic ground squirrels?

A detailed account of ground squirrel life history is provided in a later section of this chapter. However, the social, semi-fossorial (burrowing), and overwintering habits of arctic ground squirrels bestow unique characteristics which make the pursuit of several research topics (normally considered difficult or intractable) amenable to analysis. I address these three characteristics in turn.

1. Defining a study population can be a complex and difficult or a simple and arbitrary decision, depending on the purposes of study. In the case of ground squirrels, individual population units are most often considered to be a colony. Colonies are spatially discrete and do not move on seasonal (migration) or annual bases. Population units can be located with accuracy, and simple demographic metrics (density, sex ratio, age class distribution, etc.) for a given colony can therefore be tracked through time. Because ground squirrels are both sedentary and territorial, assumptions of population closure (for example during mark-recapture estimation) are achieved to a greater extent than might be possible with other animals of similar size.
2. The burrowing activities of AGS enable the estimation of contemporary and historical presence, the spatial estimation of extinction risk, and the identification of habitat characteristics that may

be associated with these estimates. The past and present occupancy of a colony may be assessed with speed, accuracy, and reasonable effort (using methods refined in chapters 2 and 4). Where evidence of past use can be found (i.e. burrow shelters that persist for decades, post use) but evidence for contemporary use cannot, the normally cryptic processes of population decline leading to localised extinction can be inferred with possibly unprecedented certainty. Here, concepts of “occupancy status” or “extinction risk” which are normally plagued by variable detection probabilities, take on an element of robustness not generally achieved in occupancy modelling. Opportunities exist to describe habitat quality in terms of the fine scale features of colonies relevant to ground squirrels.

3. Lastly, the annual cycle of AGS comprises a seasonal period of activities typical of most mammals (reproduction, growth, maturation, etc.) followed by a period of extreme inactivity during hibernation. These discrete phases of activity hold several noteworthy implications for the researcher of population dynamics. First, individuals undergoing each phase are subject to contrasting vulnerabilities to such factors as food quantity/quality and predation risk. With rare exception, direct vulnerability to predation is confined to the active season (April – October, depending on age and sex of the individual). The need for AGS to balance a minimum threshold in energy acquisition with the achievement of predator avoidance during these brief few months makes this species a good candidate for the study of how these trade-offs are managed.

Because this animal hibernates alone, the role of density dependent processes for determining overwinter survival are confined to their legacy on stored body reserves. Where individuals enter hibernation in similar body condition, differences in overwinter survival can be reasonably attributed to density independent processes acting on those individuals during the winter period. The discrete seasonal phenology of ground squirrel activity and behaviour enables

one to infer the fate of hibernating individuals with only two census intervals during spring and autumn. One may also assign all the predation recorded during the summer interval as constituting the entirety of predation for that year.

In sum, arctic ground squirrels exhibit burrowing, sedentary and hibernating systems of living which make them uniquely suited for addressing certain classes of research questions.

Theoretical issues and chapter overview

In chapter 2 I present 25 years of census data for AGS from forested habitats of Kluane, SW Yukon. Attention is drawn to the extirpation of this species in the years following their population decline of 1998-2000. The historical and contemporary trends in population density are considered in the wider context of colony occupancy and population density in non-forested habitats throughout the region.

Chapter 3 is concerned with how differences in adult female body condition between habitat types may contribute to differences in population density and population growth rates between those habitats. Early season body condition of reproductive aged female ground squirrels is a faithful predictor of reproductive output. The purpose is therefore to explore a potential partial explanation for habitat specific population growth rates previously reported for low-elevation open (meadow) and closed (forest) habitats.

Chapter 4 grapples with the etiology of extinction with an emphasis on the possible role of predation as a contributor to extirpations of ground squirrels in Kluane. Syndromes of prey abundance implicitly predicted by predator-prey theory are compared with patterns observed in per capita growth rates of AGS from 1973 to present time.

In chapter 5 the local physical characteristics of over 200 AGS colonies are measured and used to predict colony occupancy and extinction. Statistical models are therefore constructed to

isolate the potential importance (explanatory power) of each process for purpose of comparison. The potential responses of small herbivore populations to future environmental change may depend on the relative importance of food, predators, and stochastic processes such as catastrophic flooding, for determining which colonies persist through time. Those habitat characteristics correlated with extinction risk as discussed in relation to their most probable association with the fates of ground squirrel populations.

Regional description

The study area is set in the western mountains of the expansive boreal forest biome (Rowe and Halliday 1972). The winters are cold and long (October—April) and much of the precipitation is in the form of snow (40-50%; Krebs and Boonstra 2001). The Kluane area differs from surrounding boreal regions for its comparatively high elevation (valley bottoms ~840 m asl), its position in the rain shadow of the St. Elias mountains and, consequently, for its relatively cold and dry climate (mean air temperature -2.9°C, mean annual precipitation 306 mm, Environment Canada 2013).

Large tracts of the St. Elias front ranges and the geologically older Ruby ranges to the east are in receipt of loessal soils from the Slims River delta. Plant biomass and species diversity of grasslands around Kluane lake increase with the quantity of silt in the soil (Laxton et al. 1996). The unique soils of this region probably played a significant role in the vegetative productivity of the eastern Beringia ecosystem (Laxton et al. 1996) and those refugia not covered in ice during past glacial maxima (Marsh et al. 2006).

Following glacial retreat ~11,500 years B.P. a series of distinct successional stages took place beginning with sage (*Artemesia*) tundra, followed by birch shrubs (*Betula* spp. ~11,000), poplar woodlands (10,250), Juniper cover (~9,500), and finally Spruce forest (~8000) (Lacourse

and Gajewski 2000). Today the region is a mixture of open meadow and closed to open forest dominated by white spruce (*Picea glauca*). The major shrubs and woody species are willow (*Salix glauca* and *S. alaxensis*), bog birch (*Betula glandulosa*), soapberry (*Shepherdia canadensis*) and occasional shrubby-cinquefoil (*Potentilla fruticosa*). The understory is dominated by a mixture of prostrate shrubs (*Arctostaphylos uva-ursi*, *Linnaea borealis*), grass (mainly *Festuca altaica*), forbs (e.g., *Achillea millefolium*, *Anemone parviflora*, *Delphinium glaucum*, *Epilobium angustifolium*, *Gentiana propinqua*, *Lupinus arcticus*, *Mertensia paniculata*, *Solidago multiradiata* and *Senecio lugens*) and a variety of moss and lichen species (Seccombe-Hett & Turkington 2008 provide a comprehensive description of the flora).

Life history of arctic ground squirrels

Arctic ground squirrels are diurnal, fossorial rodents that live in groups of related females and territorial males (Carl 1971) that comprise colonies throughout Northern North America (Figure 1.1). Members of this species are typically active for 5-6 months of the year—the remaining time is spent hibernating in underground burrows. During the active season they defend territories and feed selectively on forbs (Batzli & Sobaski 1980, McLean 1985). Whereas males of most ground squirrel species enter hibernation in advance of females and young (e.g., McCarley 1966, Murie 1973, Michener 1977), the opposite pattern is true for AGS. Males are both the last to initiate and the first to terminate hibernation (McLean & Towns 1981, Lacey 1991). Both sexes are reproductively mature upon spring emergence as yearlings (Figures 1.2 & 1.3), and polygynous breeding occurs immediately upon female emergence (late April; Sheriff et al. 2013b). Competition among males for breeding opportunities is energetically costly (Delehanty & Boonstra 2011) and, during this time, males supplement their spring fat reserves with stored food cached during the previous summer (McLean & Towns 1981, Gillis et al. 2005).

Ground squirrels may be found at all elevations and in a variety of habitats from enclosed forests and small dry meadows (Figures 1.4 & 1.5) to the open tundra of high elevations (Figure 1.5 & 1.6). Studies from arctic and alpine habitats demonstrate that AGS populations may remain stable over short time frames of one to several years (Carl 1971, Green 1977, Batzli & Sobaski 1980).

Conceptual limitations

It is one thing to discover and describe differences between populations over time and space, but quite another to discover why such contrasts exist. Most ecological studies make quantitative statements regarding the former, while advancing only tentative conclusions concerning the latter. In this respect my work here is no different. The uncertainty which follows attempts to assign precise cause(s) to specific dissimilarities among or between populations can be understood as either resulting from the immense complexity of the system under study, or from a general desire to extrapolate beyond the confines of that system. So it is that my research comprises various attempts to confirm clusters of predictions which, even when strongly supported, nonetheless fail to confirm one preferred explanation to the exclusion of all others. While this state of affairs in ecological research should be acknowledged, it requires no apology. As is often the case with studies that attempt to explain patterns of population abundance or distribution, substitutions of time for space (and *vice versa*) have, at times, been made. Extinction patterns observed over large spatial scales are tentatively discussed in context of historical trends in a single, well studied population; and from long term data spanning decades' generalisations are advanced to account for patterns at regional scales. Where such extrapolations are made, I trust you will find that I am explicitly attentive to the uncertainties involved in this behaviour.

The various thesis chapters presented here were not written concomitantly; some minor content from a particular chapter may therefore reflect the state of my thinking or the progression of my research achieved at that time. This I believe is appropriate. Any research program is a multi-annual affair, and findings from earlier stages of the project will inform the directions of later work. For example, predation as a possible explanation for the decline of one specific population put forward in the discussion of chapter 2 was more rigorously tested in Chapter 4. The search for habitat-specificity in demography originally intended for Chapter 4 was abandoned following the results of Chapter 3, and replaced with occupancy surveys, and so on. Due to the constraints of time my thesis is also incomplete. A series of experimental re-introductions initiated during the final year of my graduate work will be written up as manuscripts for publication (described in Appendix A), but are not included as chapters in this thesis.

Tables and Figures



Figure 1.1 The approximate distribution of the arctic ground squirrels extends across northern North America.



Figure 1.2 A Male yearling arctic ground squirrel in boreal forest habitat of SW Yukon. Image taken May 22, 2014. 1/500 sec, f-8.



Figure 1.3 Adult female arctic ground squirrel approximately 15 days before entry into hibernation. Image taken August 8 2015. 1/1000 sec, f-5.6.



Figures 1.4 & 1.5 Low elevation meadow habitat of the arctic ground squirrel, SW Yukon.

Large meadows are typically situated on historic flood plains of large rivers (top panel, Duke river meadow). Smaller meadow systems such as found in Kluane National Park (bottom panel, Slims river delta region) are south facing, windswept slopes.



Figures 1.6 & 1.7 Examples of alpine habitat. Quill creek, YT (top) and Haines pass, BC (bottom). Images taken during July 2015.

Chapter 2: Arctic Ground Squirrel Population Collapse in the Boreal Forests of the Southern Yukon

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Introduction

Arctic ground squirrels (AGS) are a common small mammal in arctic and alpine tundra areas of northern Canada. One of the peculiarities of their geographic distribution is the extension of their range into the boreal forests of the Yukon (Figure 2.1). Krebs and colleagues have followed their population dynamics in the boreal forest in the Kluane Lake region of southwest Yukon since the 1970s (Hubbs & Boonstra 1997, Byrom et al. 2000, Karels et al. 2000, Gillis et al. 2005a, Donker & Krebs 2012). The characteristic feature of their population dynamics from the 1970s to 1999 was a 9-10 year cycle in numbers which was related to the snowshoe hare cycle (Krebs et al. 2014). Their numbers rose and fell during this period because they are alternate prey of the major hare predators – coyotes, Canada lynx, and great-horned owls (Boutin et al. 1995). However, after the snowshoe hare peak of 1998, AGS population density severely declined in the boreal forest by 2000, did not increase during the subsequent hare peak of 2006, and currently remains near zero. The question we address in this paper is why this collapse happened and whether it might be reversed.

Arctic ground squirrels are a pivotal species that directly or indirectly influences top-down and bottom-up ecological processes over large geographic scales in northern North America. They serve as an important prey item, herbivore and ecological engineer and their distribution drives the abundance and spatial arrangement of other ecosystem components, ranging from top

carnivores to plant communities (Wheeler & Hik 2012). In the boreal forest AGS made up 17% of the vertebrate herbivore biomass and accounted for nearly one quarter of the energy flow through the system (Krebs et al. 2001), whereas in alpine tundra, they may account for over half of the energy moving through mammalian herbivores (Wheeler 2012).

Arctic ground squirrels are the largest and most northerly distributed squirrel in North America. In arctic and subarctic regions, they form permanent social colonies comprised of shallow burrow systems (~1m depth) providing refuge from predators and thermal stress, and are used for maternal denning and overwinter hibernation (Carl 1971, McLean 1981). AGS are diurnal and consume a wide variety of grasses and forbs (Green 1977) during their five-month (range 4-7) summer active season (late April-September) prior to hibernation (Sheriff et al. 2011). The species is territorial, and populations in the montane and arctic tundra are thought to be regulated by competition for suitable habitat (Carl 1971, Green 1977, Batzli & Sobaski 1980) but in the boreal forest populations were thought to be limited by an interacting combination of food and predators (Hubbs & Boonstra 1997), and regulated by density dependent changes to overwinter survival and weaning success (Karels & Boonstra 2000). Nearly all males disperse within their first year of life, but females are philopatric and tend to settle near the natal site (Gillis 2003) unless critical resources become limiting, as has been observed only under experimental conditions (Byrom & Krebs 1999). Poor survival of juvenile males contributes to female biased adult sex ratios (Gillis 2003), and the social structure is largely polygynous (McLean 1982). A short single mating season occurs within a few days of female emergence in April (Buck & Barnes 1999a, Sheriff et al. 2011; 2013b).

Vegetation communities and soil compositions surrounding colony sites are strongly influenced by soil disturbance, selective foraging, and food caching (Gillis et al. 2005b). These

small mammals are a seasonally abundant food source for falcons, owls, hawks, Canada lynx, coyotes, foxes, wolves, and grizzly bears (Carl 1971, Byrom 1997, Gillis et al. 2005a, Donker & Krebs 2011). They are also hunted by Yukon First Nations as a traditional source of food. Population fluctuations of AGS therefore regularly affect the food supply available to these predators (Byrom 1997, Donker & Krebs 2011). Prior to the population collapse factors affecting the boreal forest population size were primarily related to changes in predation pressure, which in turn was influenced by snowshoe hare and alternate prey abundance (Gillis et al. 2005a).

In this paper we explore possible reasons for the collapse and lack of recovery of AGS populations in the forests of the southern Yukon after 2000. The scope of the present discussion is limited to the montane boreal forest of North America—the only portion of Canada’s boreal forest that is inhabited by arctic ground squirrels. We estimated abundance across a large region of south-western Yukon using mark-recapture within different habitat types and broad scale abundance surveys. We used experimental transplants into historically occupied low-elevation habitat to help us better understand the inability of AGS to recover from their current low densities. We hypothesize that predation was the proximate cause of this collapse, and that biotic factors may now prevent forest populations from recovering. Additionally, climate change may have made it lethal to hibernate in the forest because of winter and early spring rains associated with global warming. Lastly, we discuss the critical need to understand the lack of recovery of AGS populations, which may be due to their inability to colonize extinct sites.

Methods

Study area

Arctic ground squirrels occupy three distinct habitat types (boreal forest, low-elevation meadow, and alpine meadow) in the Kluane Region of the Yukon Territory, Canada. Population

data were collected at four grids: two boreal forest sites (1975-present), one low-elevation meadow site (2008-2009) and one alpine meadow site (2008-2009). In the boreal forest, most data were collected at two 10 ha grids located ~20 km from each other (~900 m above sea level (asl)) (61°00'38"N, 138°11'31"W and 60°55'53"N, 137°58'25"W) (see Gillis et al. 2005a). Both boreal forest grids were dominated by white spruce forest (*Picea glauca* (Moench) Voss) and willow thickets (genus *Salix* L.) with occasional aspen stands (*Populus tremuloides* L.). In the low-elevation meadow site, data were collected at a 10 ha grid (~800 m asl) inside Kluane National Park and Reserve (KNPR), within south facing meadow habitat surrounded by boreal forest east of the Slims River delta (60°59'56"N, 138°33'31"W). The nine ha alpine meadow grid (~1600 m asl) was also situated in KNPR and ~8 km uphill from the low-elevation meadow site in the south facing alpine meadow habitat (61°01'06"N, 138° 37'34"W). All four sites are described in detail by Donker & Krebs (2011).

Trapping and handling

At the boreal forest sites, squirrels were live-trapped on two grids each with 50 traps spaced 30 m apart in a 10 × 10 pattern with traps placed at alternate grid stations. At the low-elevation meadow site, squirrels were trapped on a grid with 50 traps spaced 50 m apart in a 5 × 10 pattern. At the alpine-meadow site, squirrels were trapped on a grid with 49 traps spaced 50 m apart in a 7 × 7 pattern. Live traps (14 cm × 14 cm × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) were baited with peanut butter. Upon first capture, squirrels were transferred to a mesh bag, tagged with monel No. 1005-1 tags (National Band and Tag Co., Newport, Kentucky, USA) in both ears, weighed, sexed, and zygomatic arch width measured using a metric dial caliper (±0.5 mm).

Density

Population density for all habitat types were obtained by mark–recapture methods. Each mark–recapture session consisted of between two (typically) or four (in situations of low AGS density) consecutive days of trapping in late July to early August. Traps were set at 0800 h, checked every 1.5 h, and closed by 1230 h each trapping day. Arctic ground squirrels are highly trappable and recapture rates were high (> 80%). All density estimates were calculated using the maximum likelihood (ML) spatial model within the program Density version 4.4 using all the default parameters (Efford et al. 2009). This model was selected because it accounts for differing edge effects associated with different grid sizes and/or layout design, and because it provides superior density estimates for small mammals (C.J. Krebs, unpubl. data).

Relative abundance

In 2008 and 2009, we indexed 18 populations of arctic ground squirrels throughout a 4000 km² area in the Kluane region, Yukon. In 2013 we indexed an additional 140 sites over a 25,000 km² area to increase our landscape perspective on the relative abundance of ground squirrels in all available habitats from the forest to the alpine (24 boreal forest habitats, 50 low-elevation meadows, 26 mid-elevation meadows, 30 alpine habitats, and 28 areas under strong anthropogenic influence such as agricultural fields and airport facilities). We used a powder tracking methodology described by Hubbs et al. (2000). Small (5 cm × 7 cm) black plastic tiles were placed in all known burrows in a specified area (typically an entire colony; minimum area = 0.5 ha if colony size < 0.5 ha, maximum area = 1.5 ha if colony > 1.5 ha – which occurred on 3 occasions) and left for six hours. The number of burrows sampled depended on the natural burrow density of the colony (mean 470/ha ± 18.2, range=56-1236/ha). The tiles were covered lightly in paraffin-based oil and unscented talcum powder. We retrieved the tiles and determined

whether the burrow was active or inactive; if the tile was moved, covered in soil or showed tracks, the burrow was considered active. The area of each site indexed was determined by recording the GPS coordinates of the corners of the site and then using MapSource (Garmin Corporation, Olathe, Kansas, USA; <http://www8.garmin.com/>, accessed 20 July 2013) to estimate the area in hectares (see Donker & Krebs 2011 for details). The area was used to calculate an estimate of active burrows/ha and total burrows/ha. In the event of a discrepancy between the number of tiles deployed and the number of tiles retrieved, the number of tiles deployed was used in the calculation of burrow density and the number of tiles retrieved was used to determine the density of active burrows. To minimize bias associated with juvenile emergence in mid-June and variation across sites, all locations were indexed between mid-May and mid-June. Since activity of arctic ground squirrels is influenced by both time of day and weather (Folk 1963), indexing was conducted between 0800 and 1600 each day during clear weather conditions. Colonies containing at least one active tile were scored as occupied, while colonies containing no active tiles were scored as unoccupied only after additional thorough investigation yielded no other sign of activity (alarm calls, recent digging, presence of clipped forage, fresh feces etc.).

Translocations

To determine whether meadow habitats serve as source populations that provide immigrants to the boreal forest dispersal was first studied from occupied sites (Donker & Krebs 2012). Specifically, 17 juveniles from low-elevation meadow and alpine tundra habitats (34 total) were radio-collared at the trapping grids previously described. Dispersing juveniles from low-elevation meadows moved further ($319 \pm 71\text{m}$ vs. $76 \pm 71\text{m}$) and had lower survival (40% vs. 90%) compared to juveniles from the alpine. Most juveniles from low-elevation meadows (11 of

17) moved into the boreal forest before being predated by raptors. We found no dispersal toward empty habitats at lower elevation sites in the forest (Donker 2010). Gillis (2003) suggested that the boreal forest might be a sink habitat for arctic ground squirrels.

To test the sink hypothesis more rigorously, in early July 2013 we moved 45 ground squirrels seven kilometres from the Burwash Airport (61°22'5.85"N 139° 1'43.10"W) to the Duke River meadow site (61°23'21.35"N 139° 6'13.86"W), a five km² habitat, containing both forest and meadow where ground squirrels had formerly been abundant but were now extirpated (Werner unpublished data). The release group consisted of 6 adult males, 17 adult females, 15 juvenile males, and seven juvenile females. At the introduction site we experimentally manipulated grass height and visibility (short grass and long grass treatments), and the number of burrows available. Treatment units were 50 x 50 m in size oriented in a 5x10 pattern (collectively treatments covered 12.5 ha of area), using a randomized block design, to maximise the use of available meadow. The entire experimental grid was trapped over four consecutive days, prior to reintroduction, during late June to confirm that it was without resident ground squirrels.

For the short grass treatment, vegetation height was reduced to 10 cm (range 0-23 cm) using gas powered string trimmers two weeks prior to the release of squirrels. The tall grass treatment consisted of un-manipulated grassland with a mean height of 94 cm (range 15-114 cm). The dried trimmings which covered <1% of the ground surface were left in situ.

To manipulate burrow density, artificial burrows (50 cm deep and 7 cm diameter) were dug using a 1½ HP gas powered auger drill and a one-piece Edelman style Dutch hand auger at a 30° angle from ground surface (similar to Gedeon et al. 2011). The low density treatment was set at

50 burrows/ha (approximating the number of natural burrows found in situ) and the high density treatment was raised to 200/ha.

Arctic ground squirrels were captured and released within 2 hours of detainment. Individuals were fitted with 1.5 g radio transmitters (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada); juveniles were fitted with expandable collars to accommodate rapid growth (see Byrom 1997 for collar construction). Capture and transport coincided with the timing of peak activity (6-10 am) observed during the previous week. To minimise social interactions with “novel” individuals the spatial arrangement among family groups (those trapped at the same burrows) at the release site mimicked the approximate arrangement at the capture site.

Radio collared individuals were located using telemetry on alternating days July 7 through August 20, 2013 in order to estimate movement patterns and active season survival. Each time a squirrel was located, its exact position was recorded using a hand-held Global Positioning System receiver (GPS) accurate to ± 5 m. All collars were removed August 19-23, 2013; translocated individuals were monitored through autumn only by visual inspection.

In addition to our experimental reintroductions, we monitored the potential for natural dispersal by immigration at five additional extirpated sites in the surrounding area to determine whether any unmarked dispersers from other meadows would settle preferentially near the release area. These five meadows, which were of comparable size to the release site and within two km of the Duke system, were trapped over two consecutive days during June 2013 (using methods previously described). These areas were subsequently monitored using repeat powder tracking every 14 days, July 10 to September 10, 2013. Burrow activity recorded in these meadows was interpreted to indicate that a dispersing animal had visited that site. Monitoring at the release site was supplemented with four camera traps (Reconyx model PC800) that recorded

still images at locations containing concentrations of telemetered animals. Cameras were placed on wooden stakes at a height of 1.2m from ground surface.

Statistical analyses

All statistical analyses were calculated using the program JMP version 4.0 (SAS institute Inc., Cary, North Carolina, USA). Differences between average densities of AGS, number of burrows/ha, and number of active burrows/ha between habitats were tested using a one-way ANOVA with Tukey's post hoc tests. Prior to analysis, all data were assessed for normality and homogeneity of variance. Both density and relative abundance data did not meet the assumptions of normality and so were transformed. A log transformation was applied to the density data and a square root transformation was applied to the relative abundance data to meet the assumptions of normality and equal variance. Standard errors for proportions were calculated using the Wilson score method (Newcombe 1998). All data are reported as means \pm SE.

Results

Density in Kluane lake region

Arctic ground squirrel density in the boreal forest underwent cyclic fluctuations from 1977 to 2000, following closely the snowshoe hare population cycle; after the population crash in 2000 AGS density remained low and did not subsequently recover (Figure 2.2). From the 1970s through the 1990s the lowest density in the forest was about 0.5 per ha in spring, typically rising to about 1.5 to 2.5 per ha in summer. After 1999 densities fell and have subsequently remained lower than 0.5 per ha, with most sites becoming locally extinct by 2009. Ground squirrels now amount to approximately 3% of the herbivore energy flow in the boreal forest zone.

Conversely, AGS populations in the alpine tundra did not collapse (Donker 2010, Donker & Krebs 2011; Figure 2.2) and were essentially identical in 1975-76 (Green 1977) and 2008-09

at 5-6 per ha (5.8 ± 0.5 in 1976 and 1977, 5.0 ± 0.57 in 2008 and 6.1 ± 0.7 in 2009; Figure 2.2). By contrast, AGS densities in the low-elevation meadow site contained about 1.5 squirrel/ha during from 2008-2009 (1.25 ± 0.22 in 2008 and 1.6 ± 0.34 in 2009), and many other low-elevation sites have become extirpated (see section below). For example, areas of low-elevation meadow along the Duke River that were formerly used by the Kluane First Nation as a favoured trapping area for fur and food were empty of ground squirrels by 2006 (G. Pope, KFN, pers. comm.) and have not returned despite a voluntary moratorium on harvesting there.

Relative abundance

A total of 158 populations were indexed throughout the SW Yukon between 2012-2013. Population density was both greater in open versus closed habitats and at higher elevations (Table 1). Occupancy rates of boreal forest sites was near zero ($4.2 \pm 0.6\%$), and many low-elevation meadow sites are locally extirpated (occupancy = $44.8 \pm 6.8\%$); whereas mid- and high-elevation populations exhibit relatively high occupancy rates ($77.6 \pm 7.9\%$ and $93.3 \pm 5.0\%$, respectively). We found that the regional densities showed a similar pattern to our intensively live-trapped areas around Kluane lake. The number of active burrows/ha (including those at inactive colonies) increased from 2.91 ± 1.21 /ha in boreal forest to 93.03 ± 17.85 in low-elevation meadow to 99.67 ± 20.70 in mid-elevation meadow, and 207.67 ± 61.44 in alpine tundra habitats ($F_{[4,146]} = 28.62$, $P < 0.0001$). A post hoc Tukey test showed that boreal forests had significantly fewer burrows per ha compared with all other habitats ($p < 0.05$) and that the alpine habitat had significantly more burrows/ha than the low meadow habitats ($p < 0.05$). An anomaly in this pattern of increasing burrow activity with elevation must be noted: ground squirrels have remained in high abundance (143 ± 26.75 active burrows/ha; Table 1) along the margin of airports (Burwash Landing, Haines Junction, Silver City, and Whitehorse) and are

reported as abundant by farmers in the Whitehorse region and in enclosed grazing land at the Yukon Wildlife Preserve outside Whitehorse. The only ecological distinction of these diverse areas is that they have a considerable amount of human activity. In some cases, such as pasture land, the natural herbivore (snowshoe hares) has been replaced by larger vertebrates (e.g. cattle, bison); in other cases, such as along aircraft runways, grass height is kept low by mechanical cutting during the growing season.

Translocations

After ground squirrels were released (n=45) 60% left the 12.5 ha treatment area and moved into forest or dense shrub cover. Of those that did not disperse into forest most displayed either an aversion to the release site (24%; i.e., the manipulated treatments), despite the provision of short grass and burrow shelters, or exhibited transient visitations to the treatment (16%) from other portions of the Duke River meadow system. Short-term survival (July 7-August 20) of translocated ground squirrels was low (~20%). All 27 squirrels that settled in forested/shrub habitats were killed by predators within 60 days, post release. Eight animals (5 adult females, 3 adult males, one yearling male) eventually settled in or near the treatment blocks or the surrounding buffer and survived to hibernation.

During late July 2013, the first records of new unmarked colonizers were obtained from camera traps positioned at active burrow complexes on or surrounding the treatment grids. Twelve adult immigrant males were identified visually at the release site and subsequently trapped and marked. Of these new recruits three adult males were captured and collared for monitoring purposes. These immigrants were observed regularly throughout the season. Regular monitoring of the five nearby control plots (to monitor immigration) in the Duke River meadow system indicated that four of the five remained unoccupied all summer. Transient burrow activity

was recorded during July at one of these control sites, but by mid-September the site was once again empty, despite the presence of adequate forage and natural burrow shelters. None of the translocated squirrels survived overwinter to spring 2014. In this experiment, we failed to successfully recolonize an area historically known as high quality habitat.

Discussion

This study makes the following observations. First, the numbers of Arctic ground squirrels present on long term trapping grids in the boreal forest decreased during the decline phase of the hare cycle, and failed to recover during the increase phase of the hare cycle. Based on population indices measured throughout the forested habitats of the Kluane region this trend of declining numbers is widespread. In forested locations where the % of burrows that are active is low, burrow density remains high, indicating that these locations recently supported greater numbers. Population density generally increases with elevation, and is higher in habitats that are open vs. closed. One notable exception to this trend are the valley bottom habitats which have been disturbed by humans and which support dense squirrel populations. Individuals that were transplanted from anthropogenic habitats to previously occupied meadows exhibited low site fidelity and low survival.

That the initial decline of arctic ground squirrel populations in 2000 coincided with the decline phase of the hare cycle points to predation—acting directly on summer survival—as the likely cause of population collapse because previous declines were found to be caused by high predator-induced mortality (Boutin et al. 1995, Byrom et al. 2000). It is less clear what mechanisms are behind the persistent low density (2000-present) and local extirpations in all low elevation habitats (Gillis et al. 2005a, Donker & Krebs 2011; Werner unpubl.). Although we do not explicitly address predator numbers, recent predator monitoring has recorded lynx

abundances during the low of the hare cycle at Kluane as being higher than ever recorded for any other previous hare low. There are more lynx in the Kluane area (and at Whitehorse) during the last several years than could be supported solely on the existing hare population (Krebs et al. 2016). These predators could either be transients seeking to avoid starvation (Ruggiero et al. 1999) or lynx have could switch to alternate prey like red squirrels during winter months (as suggested by Krebs et al. 2016). In addition to predation, climatic warming may cause hibernacula to become flooded when mid-winter rains occur, leading to high overwinter mortality. This could be catastrophic, occurring in only one year, or it could be continual over a series of winters. Possible top-down forces (both direct – killing, and indirect – nonlethal, effects of predation) maintaining low squirrel density are predicted to operate on survival and reproduction during the summer months. In contrast, bottom-up processes (catastrophic snow melt being a likely scenario) are predicted to have a pronounced effect on hibernation success in winter. Given the large-scale collapse of AGS populations at low-elevations it is also critical to understand whether AGS possess the ability to immigrate into and re-colonize extirpated sites, thus allowing populations to recover.

Predation

Hik *et al.* (2001) found that AGS were more chronically stressed in boreal forest than in continuous alpine and attributed this to the sub-lethal effects of higher predator numbers and a reduced ability for AGS to detect predators within forested areas. Direct comparisons of high alpine and low forest sites were also made by Gillis *et al.* (2005), who found that AGS in the boreal forest exhibited negative population growth, owing primarily to low active season survival and low reproduction. These findings prompted an investigation into the possible existence of source-sink dynamics between low-elevation meadows and the intervening forest

(Donker & Krebs 2012). That study was the first to compare populations in proximity, thereby controlling for the many confounding factors inherent in comparing populations across elevations (e.g., Green 1977, Hik et al. 2001, Gillis et al. 2005a, Sheriff et al. 2012). Substantive evidence for source-sink dynamics was found in that forests had negative population growth, low-elevation meadows had positive population growth, and low-elevation meadows exported dispersing juveniles into the adjacent boreal forest (Donker & Krebs 2012).

Our present understanding of AGS population dynamics in the Kluane region leaves little doubt that predation played a key role in maintaining and synchronizing population cycles of ground squirrels and snowshoe hares (cf. Boutin et al. 1995, Karels & Boonstra 1999, Byrom et al. 2000). However, it is precisely this historical cyclicity that obfuscates the interpretation of previous studies, and the relevance of those findings to all phases of the cycle or to the present non-cyclical conditions. In a sensitivity analysis of population growth in the forest population for the period 1990-2003, Gillis (2005a) concluded that population growth rate was most sensitive to small changes in adult active-season survival. Both a strong demographic Allee effect (Courchamp et al. 2008) and the existence of a predator pit (May 1977) would explain the lack of recovery after a rapid decline. In the case where the mortality agents are generalist predators (Type II functional response) Allee Effects predict population instability and increased probability of extinction. In the case where specialist predators switch between alternate prey (Type III functional response) a stable but low-density “refuge” may exist, and persistence is possible (Sinclair et al. 1998).

Climate Change

The deleterious effects of excess moisture on overwinter survival will depend on how well burrow systems are designed to protect hibernating individuals from flooding events. It must be

noted that the type of flooding whose effects are sufficiently widespread to bring about a significant decrease in regional population size can only be caused by rain-on-snow events. River flooding of the type described by Carl (1971) is restricted to habitats directly adjacent to waterways and, in a topographically diverse area like Kluane, riverbanks comprise a miniscule proportion of the habitat occupied by AGS.

Many ground squirrel species survive in relatively moist climates, where flooding is presumably a greater threat than the steppe-tundra in which AGS have resided for over one million years (Edingsaas et al. 2004). Almost nothing is known of the specific structure of hibernation burrow systems, nor of their capacity to mitigate flooding. However, Shaw (1926) describes complex drainage channels designed to draw moisture away from hibernation chambers of Columbian ground squirrels. We propose that sumps are likely a common feature of the hibernacula of other ground squirrel species whose hibernation chambers are situated in poorly drained terrain (flat hill slopes; Shaw 1926) and that these drainage features are an effective flood-mitigation technique. We find no reports of flood-induced regional population collapses of ground squirrels in the literature.

The climate-flooding hypothesis is predicated on the condition that AGS are more vulnerable to excess moisture than other ground dwelling squirrels. A key prediction, therefore, is that AGS hibernacula will lack adequate drainage tunnels to withstand surplus moisture caused by rapid snowmelt. Given their long evolutionary history (>1 million years) in the cold and arid Nearctic (Edingsaas et al. 2004), we view this loss of flood protection as distinctly possible. However, if hibernation burrows do contain drainage structures, AGS should be no more vulnerable than their southern heterospecific counterparts.

Be it noted that the present discussion addresses several possible recent proximate causes of population change. We surmise that the ultimate cause for these changes relates to climatic factors acting on temperature and precipitation regimes which themselves may be causing substantial habitat change. One such example of climatically driven change in the Kluane region is the nearly doubling of understory shrubs in forested areas, and the rapid shrub encroachment into meadows previously dominated by grass (Grabowski 2015, Krebs pers. comm. 2016).

Recovery Limitations

Given that localised extirpations are now extensive, key questions concerning the likelihood of recovery in the montane boreal are whether and how low-elevation meadows will provide sufficient immigrants to repopulate extinct locales, and whether unoccupied forested habitats can support population growth. Figure 2.3 is a hierarchical constitutive conceptual model to explain the prolonged low phase illustrated in Figure 2.2 (2000-present) and the lack of translocation success. As such, it is intended to lend coherence to future investigations of the present topic. The first question is whether dispersal occurs between populations. Most of the literature on arctic ground squirrels demonstrates strong tendencies to disperse, particularly for males (Byrom & Krebs 1999, Karels & Boonstra 1999, Gillis 2003). It is unlikely that dispersal limitation operates in this system, except possibly where the movement of females is required to recolonize extirpated colony sites. The second question is whether habitat patches are connected. The habitats around Kluane have no obvious metapopulation structure, and there would appear to be little possibility of an ecological trap (Schlaepfer et al. 2002) operating over the large spatial scale of this study. The third key question is whether vacant habitat patches are colonized. The answer to this can be both yes and no, and it is this key question that needs further discussion. We have been monitoring 10 vacant meadows since 2010 in the Kluane region and have as yet

not observed a recolonization event. Our motivation, therefore, to experimentally translocate individuals was prompted by ostensibly poor recolonization success.

Burrows are a key resource for ground squirrels (Carl 1971) and could be a limiting factor. This is unlikely, however, because the density of burrows remains at over 200 per ha at sites in the forest and over 600 per ha in the alpine. Burrows collapse slowly when not used and they remain as clear marks in the landscape for more than 25 years (Karels & Boonstra 1999, Boonstra pers. comm., Werner, pers. obs.).

When considering species in heterogeneous habitats it is necessary to address the role of habitat quality in determining dispersal rates between patches and the occupancy status of a patch at any given time (Pulliam and Danielson 1991). “Sources” are net exporters of individuals. In these high-quality habitats, natality exceeds mortality and connectivity with other habitat patches facilitates successful dispersal. In poor quality habitat or sink habitats, local yearly recruitment as driven by reproduction and survival of the patch residents is too low to sustain the population. Sink habitats are net importers and, without sufficient immigration, extinction would be inevitable. Source-sink theory is becoming increasingly nuanced in order to accommodate a growing number of empirical studies which have identified this patch dynamic in natural systems (Loreau et al. 2012). The simple “two patch” model is being replaced with scale and context specific definitions (e.g., Watkinson & Sutherland 1995) intended to explain the demographic causes and consequences of spatial movements of individuals across populations. For example, a source or sink can be “conditional” or “unconditional” (Loreau et al. 2012) depending on its intrinsic propensity to produce or absorb individuals. A source habitat may become a sink (and vice versa) over relatively short temporal scales (Boughton 1999). In

certain cases, a population may even fluctuate in and out of source-sink dynamic in a short period of time.

Source-sink theory necessarily equates habitat preference with habitat quality. Patch models assume that individuals settle in the best habitat until it fills up, with the excess being forced to settle in the inferior habitat. Optimal habitat selection therefore leads to stable population dynamics, with high population growth at low densities when nearly all individuals can settle in good habitat (Battin 2004).

For arctic ground squirrels the key question remaining to be answered in the decision tree (Figure 2.3) is whether vacant patches are colonized. One underlying question here is what defines a suitable vacant patch. There is a tendency to view this question as relating to food plants and burrow sites for ground squirrels, but an important qualification for AGS is whether there is conspecific attraction such that a suitable vacant area becomes attractive only when it is already occupied by other squirrels (Boag & Murie 1981, Weddell 1991, Reed and Dobson 1993). Weddell (1991) showed how Columbian ground squirrels will not settle in suitable habitat unless there are other squirrels already present. The observed fates of both translocated and of radio collared AGS in situ are consistent with the predation hypothesis. However, observations of unmarked immigrants after, but not before, the translocation—and to occupied but not vacant meadows—points to the possibility that the suitability of a patch [from the perspective of a dispersing individual] is at least partially determined by its occupancy status. This question might be partially tested with recorded calls of arctic ground squirrels from a tape player, or by placing caged individuals in previously unoccupied habitats and quantifying visitation rates and/or settlement behaviours of dispersing immigrants.

Ground squirrels have a kin-related social structure in which females rarely disperse and males always disperse (Lacey 1991, Gillis 2003, Byrom & Krebs 1999). Colonies of ground squirrels are thus composed of a group of related females and immigrant males. The presumed selective advantage of this social structure is based partly on alarm calls but more detailed studies in this species are needed to confirm the common belief that the alarm call is aimed at conspecifics rather than at the predator (Digweed & Rendall 2009). Male AGS are infanticidal and kin groups of females may help repel these males and improve juvenile survival (Sherman 1981, McLean 1983). A series of critical experiments are needed to sort out competing hypotheses about the use and consequences of alarm calls in this species.

Future Work

During the next two years, we intend to replicate the introduction experiments of arctic ground squirrels into areas which they formerly occupied, and to determine if they are able to escape chronic low density. Our working hypothesis is that they show an Allee effect in which densities below about 0.7 per ha cannot be sustained because of a lack of sufficient alarm calls to reduce predation mortality. In the boreal forest shrub density has increased due to reduced browsing by snowshoe hares, and shrub density prevents ground squirrels from seeing approaching predators. A key threatening process in this ecosystem is predation and successful predation is modulated by the likelihood of predator detection in dense habitats. Recent attenuation of the hare cycle and milder winter climate have allowed shrubs to expand throughout the forest region, resulting in reduced visibility and increase predation risk within the forest.

This explanation predicts that the recovery and range expansion of the AGS will first occur in open meadow habitats and in areas such as roadsides and farmland cleared by human

activities. These areas will serve as source populations for forest areas but if forest habitats remain as sinks (Gillis et al. 2005a, Donker & Krebs 2011), forest populations may never recover. This research serves to highlight changes occurring to Canada's montane boreal ecosystem. The challenges to identifying causes of population decline and barriers to future recovery are best met by addressing multiple hypotheses simultaneously.

Tables and Figures

Table 2.1. Relative abundance of arctic ground squirrels (*Urocitellus parryii plesius*) in five distinct habitat types from 2008 to 2013 throughout the SW Yukon. The density index is a measure of burrow activity using powder track methods described for this species by Hubbs et al. (2000). Occupancy is the percentage of colony sites of that habitat type that recorded a positive density index.

Habitat	n colonies	Density Index (active burrows/ha)	SE	Burrow Density (burrows/ha)	SE	Occupancy (%)	SE	Elevation (m)
Boreal Forest	24	2.91	1.21	121.2	20.2	4.2	0.6	500 - 900
Low Meadow	50	93.03	17.85	327	37.1	44.8	6.8	500 - 1000
Mid Meadow	26	99.67	20.70	494	51.7	74.6	7.9	1000 - 1500
Alpine	30	207.67	61.44	469	51.1	93.3	5.0	1500 - 2100
Anthropogenic	28	127.43	32.85	351	114.7	96.5	4.4	500 - 900

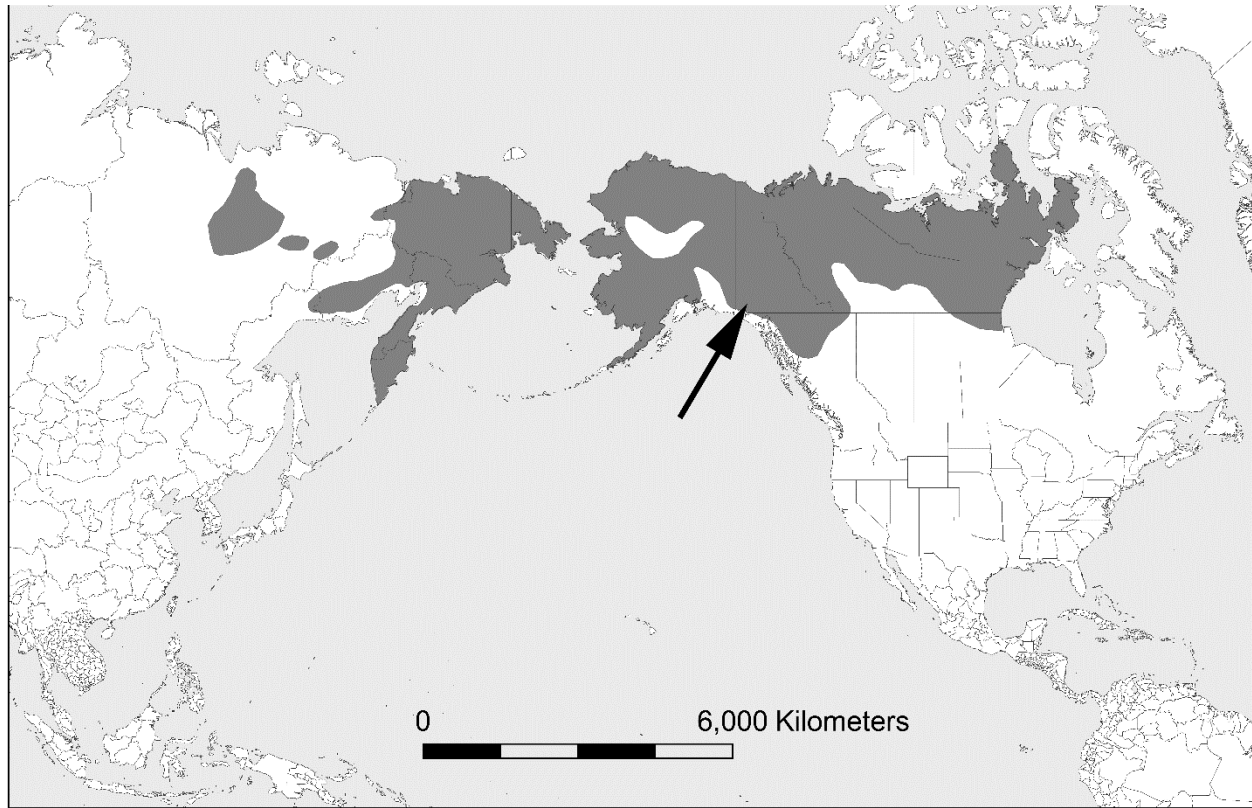


Figure 2.1 Geographical range of the arctic ground squirrel (shaded area) and the location of our studies at Kluane Lake, Yukon (arrow). Source: IUCN 2008. IUCN Red List of Threatened Species. Retrieved 8 November 2014 [<http://www.iucnredlist.org/details/20488/0>].

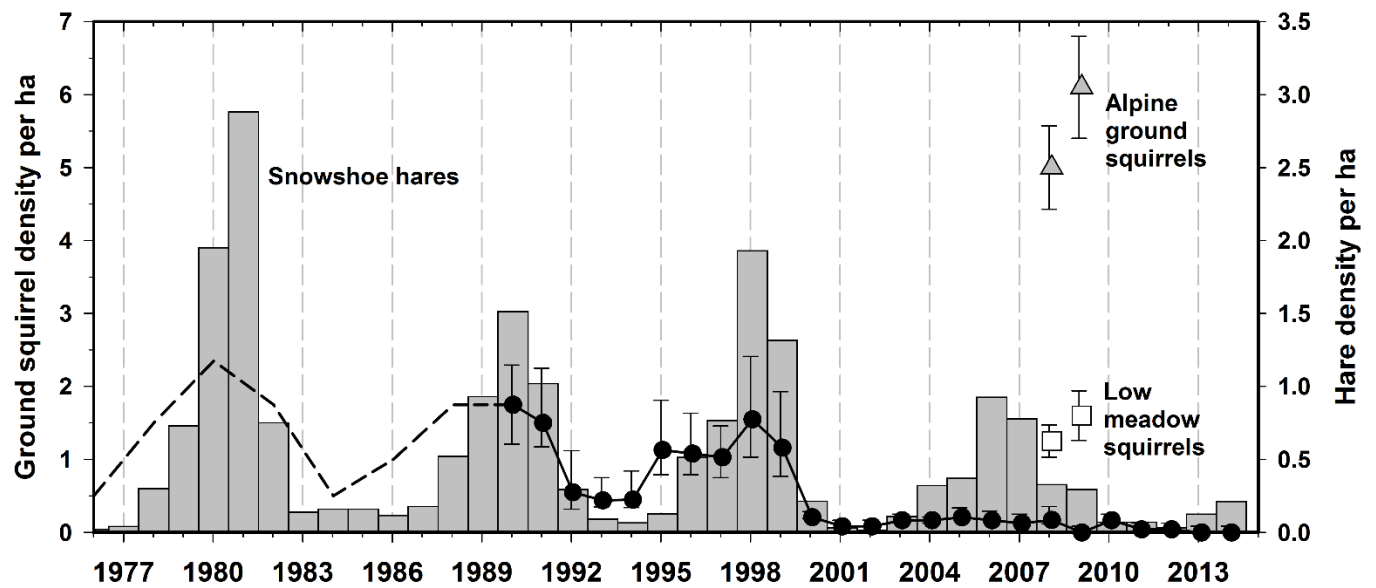


Figure 2.2 Changes in the spring density of arctic ground squirrels in two live trapping grids in the boreal forest at Kluane Lake since 1977 (filled circles) and the spring density of snowshoe hares in the same habitat (histograms). Densities of arctic ground squirrels in alpine tundra (shaded triangles) and low meadow (open squares) are from single live trapping grids during spring 2008-2009. Error bars are 95% confidence levels. The dashed line is an index of ground squirrel density obtained by correlating mark-recapture estimates to previous road count estimates conducted in Kluane 1973-1990).

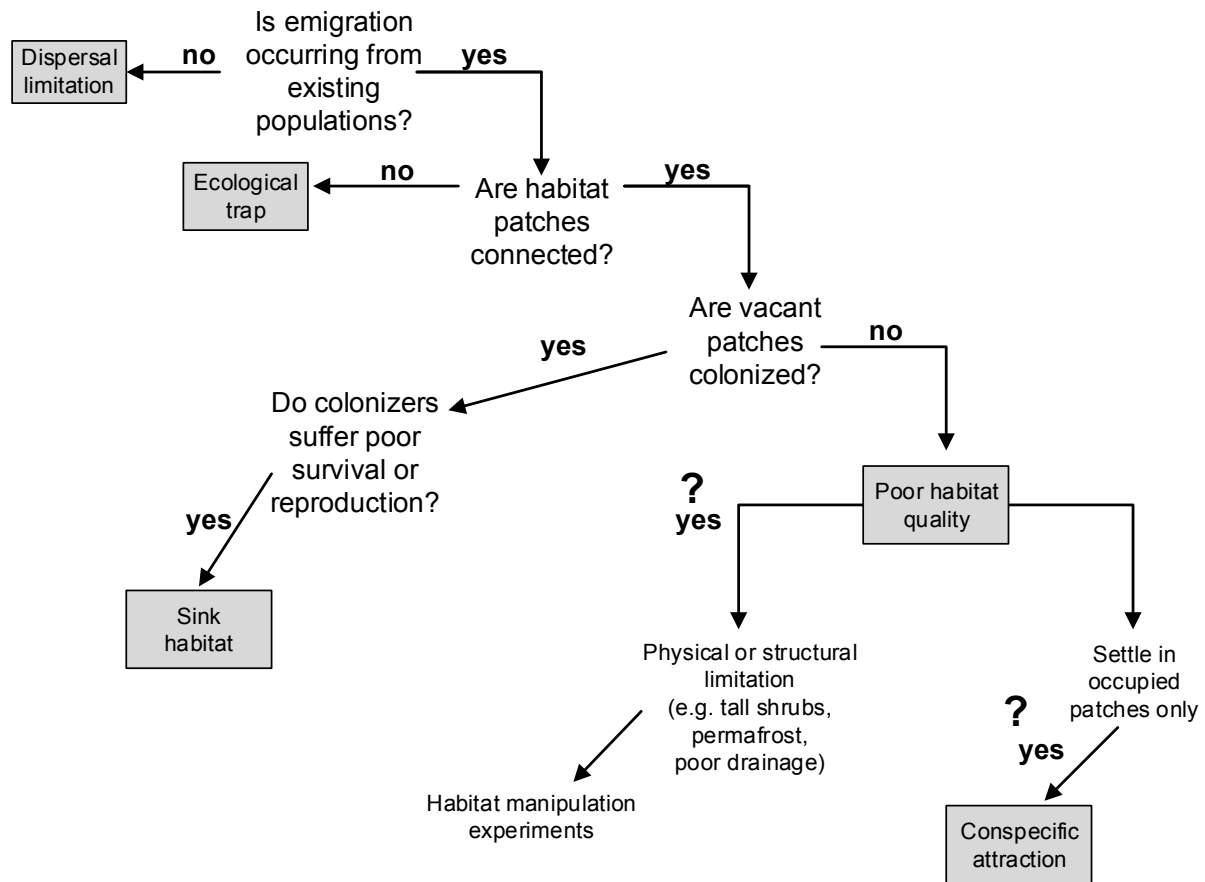


Figure 2.3 Conceptual decision tree to test for the limiting factor in arctic ground squirrel population collapses and lack of recovery over a 16-year period (1998-present).

Chapter 3: Forest or meadow: the consequences of habitat on female arctic ground squirrel condition

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Introduction

For many mammals, body mass and body condition are important determinants of overwinter survival (Murie & Boag 1984, Festa-Bianchet et al. 1997), reproductive success (Guinet et al. 1998) and susceptibility to disease (Beldomenico & Begon 2010). A positive association between stored energy reserves and overwinter survivorship in hibernating mammals has been documented extensively (e.g., Armitage et al. 1976, Murie & Boag 1984, Neuhaus 2000). Individuals that weigh more upon entrance into and emergence from hibernation reproduce more frequently and have larger and more successful litters (Rieger 1996, Millesi et al. 1999).

Habitat quality may determine the body condition of individuals who reside in different habitat patches, affecting habitat-specific demographic rates that define population “sources” and “sinks” (Pulliam 1988). In poor quality habitat, local yearly recruitment is not related to reproduction or survival rates of patch residents; these “sink” habitats are net importers and, without sufficient immigration from sources, extinction would be inevitable (Dias 1996). Source-sink theory seeks to explain the existence of space-specific demography in connected wildlife populations.

In this study, we compare spring and autumn body mass and body condition of adult female arctic ground squirrels (*Urocitellus parryii plesius* (Richardson 1825); AGS) in source and sink habitats in the boreal region of the southwest Yukon, between 2000 and 2009. Within this region, AGS occupy three main habitats - boreal forest, low-elevation meadows, and alpine tundra. Populations in the forest historically fluctuated with the 9-10 year snowshoe hare population cycle due to prey switching of specialist and generalist predators during the years when hares became scarce (Boutin et al. 1995, Werner et al. 2016). However, following the 1998 snowshoe hare peak in the Kluane region of SW Yukon, forest populations failed to recover and since 2000 have remained near zero (Werner et al. 2015a). In contrast to this dramatic disappearance, AGS in nearby low- and high- elevation meadows are common (Green 1977, Gillis et al. 2005, Werner et al. 2015a,b) and populations appear stable in these meadow habitats (Donker & Krebs 2011). We evaluate two broad hypotheses to explain the observed habitat-specific dynamics.

Hypothesis 1: Source and sink habitats differ in feeding conditions, and either low reproduction or high overwinter mortality generates sink demography. From this we predict that AGS in source habitats are in better body condition both when entering hibernation and soon after emerging the following spring, compared with AGS in sink habitats.

Hypothesis 2: Source-sink dynamics are driven primarily by active season mortality, possibly predation. From this we predict no significant differences in body condition of AGS from source and sink habitats when individuals enter hibernation and after emergence the next spring.

Methods

Study species

AGS are the largest and most northerly distributed of all ground squirrels in North America (Naughton 2012) where they occupy arctic tundra, alpine areas, and the montane boreal forest of northwestern Canada and Alaska (Nadler & Hoffmann 1977, Naughton 2012). They are active for only 3-5 months per year and the majority of their life history comprises a 7-9 month hibernation period lasting from as early as mid-August to as late as late May (McLean & Towns 1981). Females breed within days of spring emergence (mid-April) and produce a single litter ~25 days later (mid-May) (Green 1977, Lacey et al. 1997, Karels et al. 2000, Sheriff et al. 2011). Juveniles are weaned and emerge from their natal burrow in mid/late June. Nearly all males disperse, whereas most females settle within their natal home range (mean dispersal distance for males and females was 515m vs. 120m; Byrom & Krebs 1999). Adult females are at their lowest body mass at emergence and, in arctic tundra, mass does not increase for the first month (Buck & Barnes 1999a, Sheriff et al. 2013a); however, in SW Yukon adult females are reported to accrue mass immediately after emerging from hibernation and continue to do so through parturition (McLean & Towns 1981).

Study area

Arctic ground squirrels were studied in the Kluane Region of the Yukon Territory, Canada in two valley bottom habitats, boreal forest (~900 m asl) and meadow (~800 m asl). In the boreal forest, data were collected from 2000-2009 on two live-trapping grids (~900 m asl; N 61° 00' 38'' W 138° 11' 31'' and N 60° 55' 53'' W 137° 58' 25'') located ~20 km from each other. These grids were dominated by white spruce forest, small clearings, and willow thickets with occasional aspen stands (described by Krebs et al. 2001 and Gillis et al. 2005). In the meadow (~10 ha in

size), data were collected from 2008-2009 on one grid dominated by grasses and surrounded by boreal forest (described by Green 1977 and Donker & Krebs 2011). On the boreal forest grids AGS population density was $0.38 \pm 0.13/\text{ha}$ (all age/sex classes combined) in 2000 and declined to extirpation by 2009; in the meadows AGS density was stable between 2008 and 2009 at $1.25 \pm 0.22/\text{ha}$ (Donker & Krebs 2011).

Trapping and handling

In the boreal forest, AGS were captured on 10 ha grids with traps spaced 30m apart in a 10x10 pattern with traps placed at alternate grid stakes. The number of unique adult females captured over the entire ten-year period was 45 and 36 during spring and autumn, respectively. At the meadow site, squirrels were captured on a 10 ha grid with traps spaced 50 m apart in a 5x10 pattern. The number of unique females captured during spring and autumn was 24 and 17. These numbers reflect the low population densities at both sites (see below).

Each year, trapping was conducted for four consecutive days between May 21-29, from 0700h to 1100h (except in 2009 where trapping at the meadow site was extended to 5 consecutive days in response to cold temperatures and low capture success). Autumn trapping was conducted August 1-11, and consisted of between two and four consecutive days of trapping. We used Tomahawk live traps (14 x 14 x 40 cm, Tomahawk live trap Co., Tomahawk, Wisconsin) baited with peanut butter. Upon capture, adult females (yearlings excluded) were transferred to a mesh bag, tagged with monel No. 1005-1 tags in both ears (National Band and Tag Co., Newport, Kentucky), weighed with a Pesola spring scale (accurate to $\pm 5\text{g}$), sexed, and skull width measured ($\pm 0.5\text{mm}$). This research was approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council for Animal Care.

Statistical analyses

We used a two-way ANOVA to test for the main effects of season and habitat, as well as the interaction of season and habitat on mass patterns at parturition and prior to entrance into hibernation. To determine the body condition of adult females, we obtained the residuals of body mass (g) regressed on zygomatic arch width—a reliable estimate of skeletal size (Dobson 1992, Dobson & Michener 1995, Karels 2000, Schulte-Hostedde et al. 2005) with simple linear regression using ordinary least squares. Jakob et al. 1996 and Schulte-Hostedde et al. (2005) assessed techniques for determining body condition and report that this method performs best. We then used this metric of body condition in a second model to investigate the effects of habitat and season on adult female AGS body condition. Differences between mean residuals were tested using a two-sample t-test. All statistical analyses were calculated using program JMP v4.0 (SAS institute, Cary, NC). Prior to analysis, data for mass and size were assessed for normality and homogeneity of variance (Shapiro-Wilk test) and subsequently log-transformed. No significant inter-annual differences in mass or condition were found among years within each habitat type and data were pooled. Further, to explore the seasonal relationships between body mass and condition, we obtained r^2 values for regressions of the residual index on body mass. All data are presented as means (back transformed) \pm SE.

Results

Body mass and size

We found a significant main effect of both season ($F_{[1,121]}=140.564$, $P<0.001$) and habitat ($F_{[1,121]}=9.814$, $P=0.002$) on the mass of adult females. There was also a significant interaction between the effects of season and habitat type on the mean mass of adult females ($F_{[1,121]}=4.859$, $P=0.029$; Figure 3.1). Overall, females increased their body mass from late May to early August

by approximately 25%. In the meadow, females were 8% heavier in spring than those in the boreal forest (meadow=437g \pm 11, forest=405g \pm 7) but, by autumn body mass was comparable (meadow=520g \pm 15, forest=519g \pm 13).

We found a significant main effect for season on structural size ($F_{[1,121]}=13.360$, $P<0.001$), and a slight main effect of habitat on size ($F_{[1,121]}=2.914$, $P=0.09$). No interaction effect of habitat and season were detected ($F_{[1,121]}=0.011$, $P=0.9$). Overall, adult females were ~3% larger during autumn than during early spring (mean zygomatic arch breadth; spring meadow=33.09mm \pm 0.23; spring forest=33.54mm \pm 0.32; autumn meadow=34.12mm \pm 0.22; autumn forest=34.63mm \pm 0.21).

Body condition

Body condition of adult females was estimated as the residuals in a regression of seasonal body mass on structural size (zygomatic arch breadth). The first model using spring body mass regressed on skull width was significant ($y=11.05x+26.23$, $r^2=0.11$, $n=69$, $F=6.57$, $P=0.01$). The second regression model of autumn body mass on skull width was also significant ($y=2.45x-1.06$, $r^2=0.38$, $n=51$, $F=31.6$, $P<0.001$). These results indicate that size explains more of the variation in mass during autumn than during spring (~3.5x). The residuals from these models are, by definition, independent of size (confirmed by inspection of residual plots). We then compared the mean values of these residuals between habitats and found that female AGS who reside in the boreal forest had lower spring body condition (mean residual = -11.0 \pm 10.2g) compared to those in meadows (mean residual = 20.5 \pm 6.1g; Figure 3.2) ($t_{[68]}=2.47$, $P=0.01$). In autumn, forest females also had lower, but not significantly different, body condition (mean residual = -0.01 \pm 0.01g; Figure 3.3) than meadow females (0.03 \pm 0.01g) ($df=51$, $t=-2.76$, $P=0.8$). Winter conditions during 2007/2008 and 2008/2009 (the period during which meadow data were

collected) were characterized by relatively little snowfall and cold temperatures (Figure 3.4). Any yearly biases in spring mass caused by poor hibernation conditions during this time will result in an underestimate of reported differences between habitats.

We found that the relationship between mass and condition changed with season. During spring, body mass was a very good predictor of body condition in both habitats (forest condition regressed on mass $r^2=0.87$, meadow $r^2=0.97$; Table 3.1) but the strength of these correlations decreased by onset of autumn (forest $r^2=0.58$, meadow $r^2=0.66$; Table 3.1). Where spring data on condition of adult female ground squirrels are lacking, measures of mass (regardless of structural size) may therefore serve as a useful surrogate. This unexpected result may have profoundly useful implications for other ground squirrel researchers who possess standard records of spring mass but not size (and can therefore not calculate body condition).

Discussion

Despite wide recognition linking patterns of seasonal mass gain and body condition with survival (Armitage 1981, Festa-Bianchet et al. 1997, Cook et al. 2004), reproduction (Clutton-Brock et al. 1986, Barash 1989, Guinet et al. 1998) and population growth (Kilgore & Armitage 1978, Ozgul et al. 2010), and despite the acknowledgement of habitat-specific demography in AGS (Gillis et al. 2005, Donker & Krebs 2011), this constitutes the first comparison of mass and condition between adjacent habitat types. Our results support our hypothesis that adult female squirrels in sink habitat (forest) weigh less (Figure 3.1) and are in worse condition (Figure 3.2) in spring compared to those in source meadows. However, these differences did not persist into autumn and both forest and meadow squirrels were of similar mass and condition just prior to entering hibernation.

What causes differences in spring body mass and condition?

We identify three plausible, non-exclusive, causes for these inequalities in mass and condition. First, heightened mass gain may be a direct benefit accrued to females who do not successfully reproduce. Unsuccessful females avoid the energetic expenditure associated with lactation and rearing of young and may begin mass gain far earlier in the season, giving them a substantial advantage as far as mass gain is concerned. However, we view this explanation as unlikely because these non-reproductive females should be heavier by late May as a consequence of these energetic savings accrued during the previous month.

Secondly, this may be a consequence of environmental conditions during the early spring. At this initial stage of the vegetative growing season forbs have not yet emerged, and AGS must forage on woody browse, seeds, and dead grass from the previous summer. Persistent snow cover will directly interfere with a squirrel's ability to encounter these food items, while further delaying plant phenology and, thus, the quantity of available forage during May. Habitat-specific mass patterns may therefore be governed by habitat-specific foraging opportunities.

Lastly, differences in mass and condition may reflect the overwintering environment. We suggest that forest squirrels may face greater physiological demands during hibernation that result in poor spring body condition. In the forest females select small open areas as hibernation sites, presumably because snow accumulation and soil temperatures are greater (Karels 2000). Because female AGS are sedentary (Byrom & Krebs 1999) and openings make up only ~25% of the area in the forest, differences in the availability of optimal hibernacula between forest and meadow habitats may contribute to differences in spring body condition observed between habitats (but see Buck and Barnes 1999b). We do not directly test these competing hypotheses

and, although they warrant further scrutiny, we emphasize that contemporary density of squirrels in boreal forest habitats (~0 individuals/ha) does not permit such study.

One important limitation not explicitly considered in this study is the possible effect of differences in mass or condition-specific survivorship between habitat types. Were smaller individuals in forests, for example, to experience lower summer survival then autumn estimates of female mass would be skewed towards larger individuals. This confounding possibility could be addressed by following the fates of specific individuals from spring through autumn.

What are the consequences for habitat-specific body mass and condition?

Body mass

Adult female AGS living in the forest weighed significantly less, during spring, than squirrels that lived in nearby meadow. However, by the onset of entrance into hibernation females in both habitats weighed the same (Figure 3.1). Demographic implications of low spring mass for female ground squirrels are low reproductive success and small litter sizes, but also increased overwinter survival because lighter individuals are unlikely to bear the energetic costs of reproduction (Rieger 1996, Millesi et al. 1999, Karels et al. 2000). For example, female Columbian ground squirrels (*Spermophilus columbianus*) that are lighter during spring will often not reproduce, but experience greater subsequent overwinter survival compared to heavier females that successfully raise litters (Neuhaus 2000). Similarly, Donker & Krebs (2012) found that AGS overwinter survival was higher but reproduction was lower in the boreal forest than in meadow habitat.

Body condition

We also found that adult female AGS in forest (sink) habitat were in worse condition, during spring, than those in nearby meadows. Differences in the body condition of females can

have pronounced population level consequences directly, via reduced survivorship, and indirectly via reduced reproduction (Dobson & Michener 1995). Studies of Richardson's ground squirrels (Dobson & Michener 1995) and Columbian ground squirrels (Skibiell et al. 2009) found that mothers in worse body condition produced fewer young and that female offspring from these smaller litters were less likely to survive their first winter.

Poor body condition may also increase an individual's vulnerability to predation, particularly if the focal species is a secondary prey item to a dominant predator. For red squirrels in Idaho (*Tamiasciurus hudsonicus*), a system where snowshoe hares were the primary prey species, those in poor condition were more intensely predated (Wirsing et al. 2002). In the Yukon boreal forest, AGS are a secondary prey with snowshoe hares again being the primary prey. In this system, squirrels who are in poor condition also experience higher predation (Donker & Krebs 2011).

It is instructive to note that during spring (and regardless of habitat) body mass correlated highly with body condition ($r^2=0.87-0.97$; Table 3.1), such that comparisons of mass alone would have served well for this study. The strong redundancy observed during spring between mass and condition weakens as individuals undergo variable rates of pre-hibernation fattening (August $r^2=0.58-0.66$); we therefore caution against the use of similar substitutions during autumn.

Mass gain

A fundamental challenge for prey is to achieve a minimum energy balance (in the case of AGS and all hibernators it must be positive over the course of an active-season) while minimising predator encounters. This conflict is central to an understanding of individual behaviour (Lima & Dill 1990) and habitat-specific distributions of wild populations (Brown

1988). Food acquisition and escape are often considered as trade-offs, expressed by the opposing activities of foraging and vigilance. The key question here is what costs are incurred by forest females who maintain a greater active-season growth rate, to achieve similar pre-hibernation mass, compared to those females inhabiting meadow habitats.

As arctic ground squirrels *must survive hibernation* if they are to breed, we should expect them to tolerate higher predation risk if it will help minimize overwinter mortality (Karels et al. 2000) (*sensu* the predation-starvation hypothesis; McNamara & Houston 1990). In a study by Karels et al. (2000) predation risk was manipulated through large (~1km²) exclosures and the reproductive behaviour of female AGS was measured. The lower reproductive success on control grids, and superior weaning rates in predator exclosures (Karels et al. 2000) point to the sub-lethal effects of mammalian predators (Preisser et al. 2005) in the boreal forest system. Moreover, despite predator exclusion improving female body condition and subsequent reproduction, the authors found no effects of predator exclusion on overwinter survival (Karels et al. 2000). In light of habitat parity in autumn mass (our study), and the lack of evidence linking more food and fewer predators to better overwinter survival in the forest (Hubbs & Boonstra 1997, Karels et al. 2000), adult mass gain appears strongly compensatory. Overwinter survival ‘at all costs’ is likely an essential life-history strategy for this and other hibernating species.

Negative population growth (Donker & Krebs 2011) and low colony occupancy (~4%; Werner et al. 2015) are contemporary features of forest AGS of SW Yukon. We hypothesize that being in poor spring body condition may influence reproduction and active-season survival. Ground squirrels under heightened pressure to achieve sufficient fat and muscle reserves (Boonstra et al. 2014) to survive a long hibernation period likely forego strategies that maximise short-term survival (vigilance), for behaviours intended to ensure successful hibernation

(foraging). The prioritisation of foraging over safety could be expressed in two ways. First, adult females will devote more of their above ground activities to foraging (presumably at a cost to vigilance behaviour; Lima & Bednekoff 1999). Second, vigilance is maintained while total time spent above ground is lengthened—either as the fraction of daily activity or by delaying hibernation. These predictions can be tested by obtaining activity budgets and dates of late summer immergence. There are currently insufficient numbers of AGS in forests of this region to test this foraging-vigilance hypothesis.

In summary, we found females had lower spring mass and were in poorer body condition in the boreal forest compared to those in meadow; these circumstances are associated with low reproductive success and reduced summer survival (Gillis et al. 2005, Donker & Krebs 2011). However, boreal forest females exhibited compensatory mass gain during the active season. We submit that females with elevated rates of mass gain must prioritize long-term energy storage over short-term safety, and that this shift may further exacerbate predation risk in the boreal forest (Hik et al. 2001, Gillis et al. 2005a). Alternatively, forest females may be able achieve greater mass gain because of their poor reproductive success and lack of energy expenditure required for gestation and lactation. Further, in northern ecosystems global warming is predicted to intensify this trade-off, as the role of predation in regulating small herbivores increases (Legagneux et al. 2014). These factors may contribute, in concert, to maintaining the source-sink relationship between the forest-meadow habitats and also to the recent population collapses of ground squirrels (Werner et al. 2015a) in the Kluane region.

Tables and Figures

Table 3.1 Coefficient of determination for seasonal linear regressions of body condition (residual index) over Log body mass (g) of adult female arctic ground squirrels in low elevation meadow and boreal forest habitats during May and August, 2000-2009, SW Yukon.

	Spring r^2	n		Autumn r^2	n	
Boreal Forest	0.87	45	$y = 16.33x - 42.619^*$	0.58	36	$y = 8.8527x - 23.747^{**}$
Low Meadow	0.97	24	$y = 16.33x - 42.619^*$	0.66	17	$y = 8.8527x - 23.747^*$
Combined	0.86	69	$y = 15.764x - 41.024^*$	0.62	53	$y = 0.6171x - 1.6534^*$

*Significant at $P < 0.001$ **Significant at $P < 0.01$

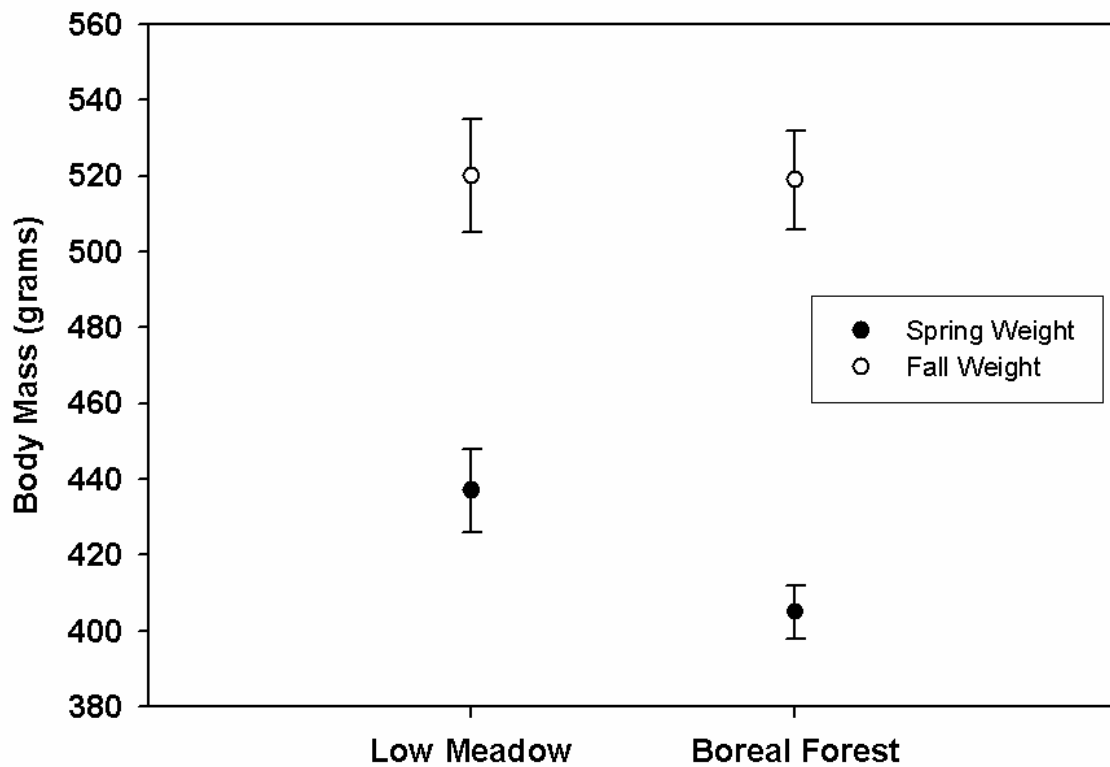


Figure 3.1 Adult female arctic ground squirrel spring and autumn body mass (mean \pm 95% confidence intervals), in boreal forest and low-elevation meadows of the Kluane region, SW Yukon. (Spring: 437 g low meadow ($n=24$), 405 g boreal forest ($n=45$). Autumn: 520 g low meadow ($n=17$), 519 g boreal forest ($n=36$); t -test: $df=55$, $t=2.40$, $P=0.02$).

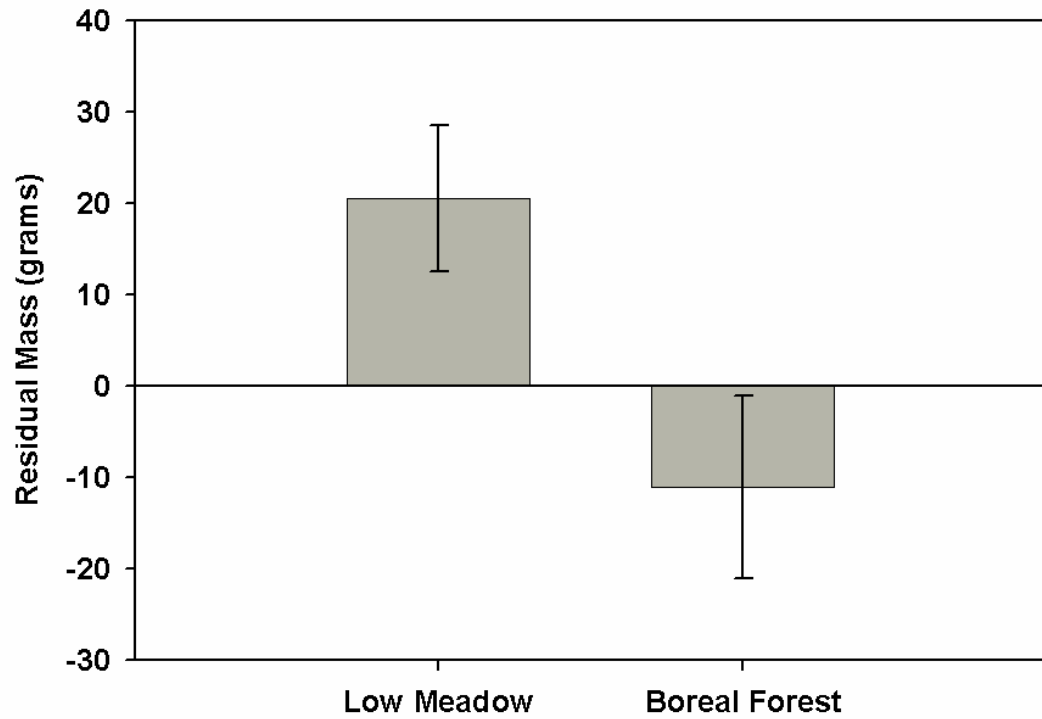


Figure 3.2 The spring body condition index of adult female arctic ground squirrels in two contrasting, low elevation (~800 m) habitats boreal forest and low-elevation meadows of the Kluane region, SW Yukon. Bars represent 1 SE (low meadow: 20.5 g, boreal forest: -11.0 g; t -test: $df=68$, $t=2.47$, $P=0.01$). $n=45$ for boreal forest and $n=24$ for meadow.

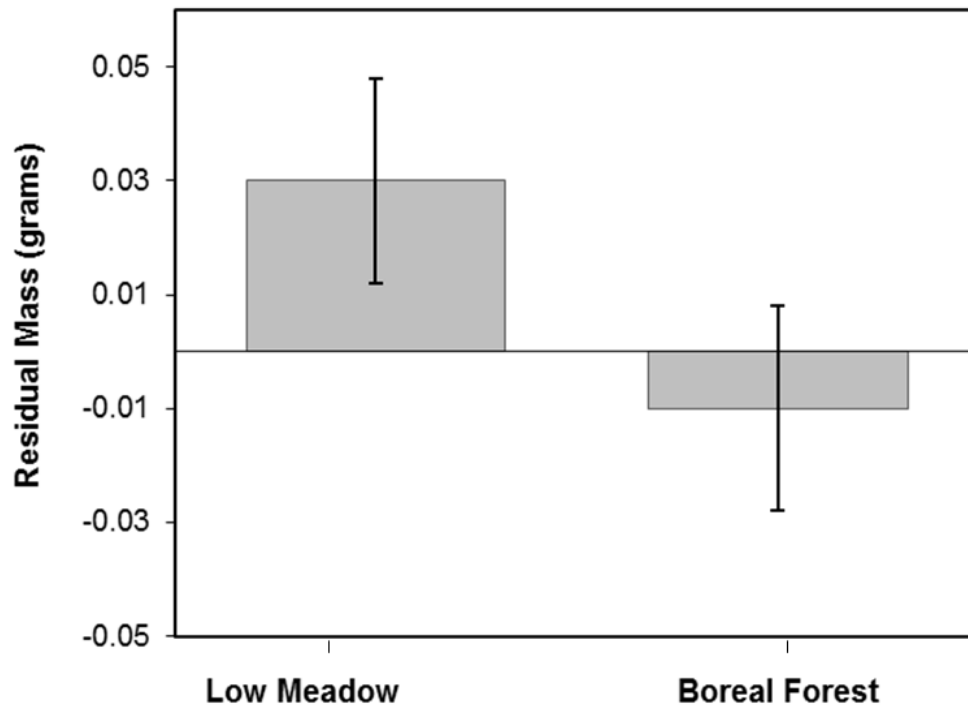


Figure 3.3 The autumn body condition index of adult female arctic ground squirrels in two contrasting, low elevation (~800 m) habitats boreal forest and low-elevation meadows of the Kluane region, SW Yukon. Bars represent 1 SE (low meadow: 0.03 g, boreal forest: -0.01 g; *t*-test: *df*=51, *t*=2.76, *P*=0.8). *n* =45 for boreal forest and *n* =24 for meadow.

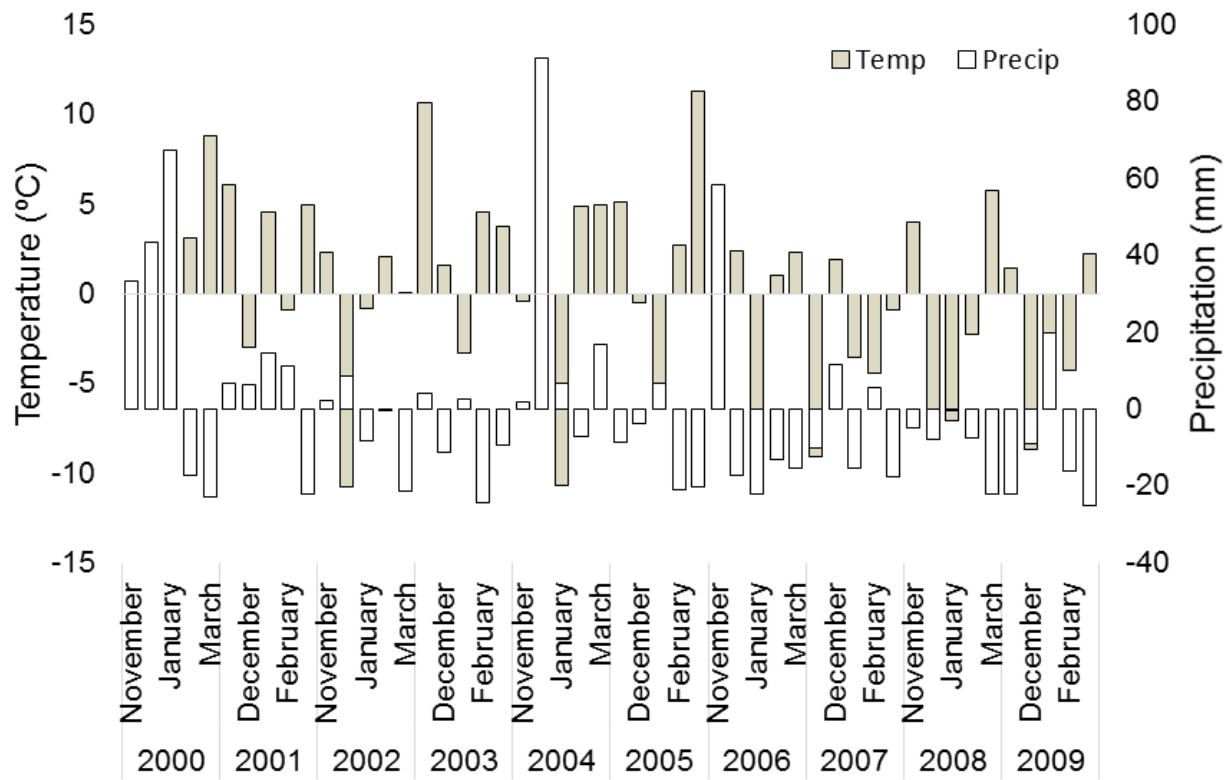


Figure 3.4 Difference in mean monthly temperature (grey) and precipitation (white) from long term average (1980-2009). Source: Haines Junction Airport Meteorological station, Environment Canada. Mass data collected during 2008-09 from low-elevation meadow habitat are represented by relatively low temperatures and snow cover.

Chapter 4: You can hide but you can't run: indirect effects, predator responses and the decline of Arctic ground squirrels in boreal forests of the southwest Yukon.

This chapter has been peer reviewed and published as the following article:

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Introduction

The comprehensive role that snowshoe hares (*Lepus americanus*) play in the food web dynamics of North America's boreal forest epitomizes the notion of "foundation species" (sensu Dayton 1972) who by virtue of their abundance and influence on other species helps define an entire ecological community (Sinclair & Krebs 2001). In particular, the cyclic oscillating abundance of the hare and its predators (e.g., lynx, coyotes, great horned owls) is central to our understanding of how predators influence the population dynamics of other common prey species in this system (Boutin et al. 1995).

Predator-mediated indirect effects (Holt 1977, Wootton 1994) between two prey can occur when at least one natural enemy is held in common and, that enemy enables the numbers of one species to negatively influence the abundance of another. In the case where such negative influences have a stronger effect on the secondary prey species, 'asymmetric' indirect effects can lead to a variety of outcomes that depend on the intrinsic nature of the predator-prey relationship (Sinclair & Pech 1996, DeCesare et al. 2010). Additionally, when predator-prey systems are routinely not at equilibrium, the primary prey species may achieve rapid increase leading to predator satiation and a temporary decrease in the per capita predation rate for both prey species

(Holt & Lawton 1994, Abrams & Matsuda 1996). The effects of predator satiation, however, are limited to short time scales, because the higher availability of prey will trigger a numerical response in the predator over subsequent predator generations (Holt & Kotler 1987). Although the influence of such positive indirect effects is generally fleeting, this effect may recur when population densities of the primary prey show cycles that result in repeated satiation of the shared predators and reduced predation on the secondary prey species (Abrams et al. 1998, Norrdahl & Korpimäki 2000). The periodic intensification and relaxation of predation is implicated in the synchronous population fluctuations of voles and either hares (Angelstam et al. 1984) or grouse (Hörnfeldt et al. 1986) in Sweden, voles and shrews in northern Europe (Hansson 1984, Korpimäki et al. 2005), small rodents and ground nesting birds in northern Eurasia (Sutherland 1988) and the high arctic (Bêty et al. 2002), and hares and ground squirrels in the Yukon (Byrom et al. 2000). The alternating influence of prey switching during the decline phase of the cycle, followed by escape from predator regulation during the increase phase, are sufficient conditions for synchronous cycling of primary and secondary prey (Abrams et al. 1998, Norrdahl & Korpimäki 2000).

In North America dramatic fluctuations in hare density are also known to entrain other prey species into cycles of similar duration (Boutin et al. 1995, Krebs, Boutin & Boonstra 2001). The best documented case is that of the arctic ground squirrel (*Urocitellus parryii*; hereafter AGS), whose numbers in the SW Yukon varied in synchrony with hares for over three decades (Werner et al. 2015a). The putative mechanism for these coincident patterns in abundance is prey-switching, from hares to ground squirrels, during the decline phases of the hare cycle (Boutin et al. 1995, Byrom et al. 2000, Krebs et al. 2014).

These forest ground squirrel populations and their cyclic patterns have been investigated since the 1970's (Green 1977, Hubbs & Boonstra 1997, Byrom et al. 2000, Karels et al. 2000, Gillis et al. 2005, Donker & Krebs 2012). From the 1973 to 1999 increases among AGS have been stopped by declines that recur with near decadal regularity. However, after 2000, AGS populations declined rapidly at lower elevations (~900m asl) in the Kluane region (Donker & Krebs 2011), and colony extirpation is now widespread throughout similar habitats of the southern Yukon (colony occupancy = 4.2%; Werner et al. 2015a Table 1). The range of this historically ubiquitous herbivore appears to have contracted over the course of a decade. Werner et al. (2015a) hypothesized that this abrupt shift in squirrel abundance, followed by a prolonged phase of very low numbers, was diagnostic of predator regulation (i.e., a 'predator pit' whereby a prey population is maintained at a lower stable equilibrium point well below carrying capacity). However, no direct evidence to support this claim was offered at that time. Here we test whether the observed population dynamics of AGS are consistent with patterns predicted by predator-prey theory.

To predict whether this historically common herbivore (Boonstra et al. 2001) might regain a foothold in this system requires an explicit understanding of the predator response, especially as it relates to low prey density (Sinclair & Krebs 2002). In cases where a prey population's growth is most sensitive to changes in survival (as is the case with this AGS population; Gillis et al. 2005a) and where prey mortality is almost entirely caused by predation (as is also the case with this population; Hubbs & Boonstra 1997), the predator response can be determined by inspection of the instantaneous rates of change in the prey species over a realistic range of densities. Such analyses across a wide range of taxa (Messier 1994, Sinclair et al. 1998) confirm two general categories of predator response curves predicted by predator-prey theory (Holling

1959, Holling 1973, Sinclair & Pech 1996). Where predators suppress but do not eliminate prey at low density (Type III predator response; Figure 4.1), persistence of the prey species is possible, as is the potential for population recovery in the absence of harmful stochastic events or strong fluctuations in food availability. Even where localised extirpations have occurred, habitat recolonization via immigration is possible. In contrast, when predators continue to consume prey at low prey availability (Type II predator response; Figure 4.1) local extinction may be inevitable. Discriminating which of these two classes of predation are in operation is an important first step towards ascertaining the fate of this single, well studied AGS population in the boreal forest ecosystem. Unlike chapters 2, 3, and 5 which document patterns across many populations, the present study is limited to the control grids used during the Kluane Lake Ecosystem Project (see Krebs et al. 2001). While patterns drawn from this study may be limited in their application to the wider region, the published demographic data for these hare and AGS populations span the necessary time interval to satisfy our analytical assumptions.

Our purpose is to document a change in the strength of indirect interaction between a sympatric population of hares and arctic ground squirrels and to clarify the recent influence of predation in controlling ground squirrel numbers during the later stages of their disappearance. Both aims are met in this paper by analyzing over two decades of long-term population census data collected for hares and AGS in the Kluane region of the SW Yukon. Strong correlation between primary and secondary prey numbers across a wide range of population densities is a common outcome of predator induced cycles (Korpimäki et al. 2005). Furthermore, the population trajectory of the ground squirrels at various population densities provides useful information concerning population dynamics at low prey numbers (Sinclair et al. 1998). We

evaluate the following hypotheses to account for the observed changes in ground squirrel abundance over a 25-year period:

Based on a visual inspection of census data (near decade long persistence at very low density) we hypothesized a Type III predator response (Figure 4.1). [Note: a declining slope in the per-capita population growth curve as it crosses the zero line in Figure 4.1 is generally indicative of some form regulation]. This hypothesis maintains that AGS populations have two possible stable states: one where they are regulated below their carrying capacity by predators, and one where they are regulated at higher numbers by density-dependent mechanisms associated with nearing carrying capacity (Sinclair & Pech 1996). This would explain the apparent shift in AGS abundance to a persistent lower population size after 2000. Predictions are that the summer (May—August) per capita growth rate of the prey plotted over prey density will exhibit two positive equilibrium densities separated by a boundary threshold. The alternative hypothesis is that the predator response is Type II. AGS populations are unstable at low density (de-regulated by predation) but escape predation at high density. This hypothesis predicts the existence of a single upper stable population equilibrium and a single lower unstable boundary below which prey density declines towards extinction (i.e., inverse density-dependence; Figure 4.1). We additionally hypothesized that the AGS population was, at all times, governed by predator-mediated competition with hares followed by repeated escape from predator control. This hypothesis predicts a singular association between the annual census data of hares and ground squirrel throughout the monitoring period. *A priori* knowledge of the system indicates that this is quite likely (Karels et al. 2000, Sinclair & Krebs 2001). However, the correlation dynamic may also have weakened with time. The alternative hypothesis is therefore that a phase-change occurred after 2000, causing the system to shift from predator-mediated competition to a

new state unaffected by hare numbers. This ‘multi-state’ alternative predicts an uncoupling in the strength of correlation between hare and squirrel density after 2000.

The distinguishing predictions for these hypotheses can be tested, given that two assumptions are correct: 1) changes to AGS numbers during the active season are not affected by overwinter mortality (as might be the case if using annual census data only). 2) Population trajectories are most sensitive to changes in survival. 3) The bulk of active season mortality can be attributed to predation. The first statement is axiomatic; the second and third are supported by past studies that, incidentally, contributed to the data set presently being analyzed (i.e. same trapping grids and over the same time interval of this study). For the period 1992-2003 population growth rates are most sensitive to changes in adult active-season survival (Gillis et al. 2005a), and 93-100% of active-season (summer) losses of radio telemetered AGS are confirmed predator mortalities (93% Hubbs & Boonstra 1997; 96% Byrom et al. 2000; 100% Donker & Krebs 2012; 100% Werner et al. 2015a). Hubbs (2003) illustrates the importance of predation for controlling ground squirrel numbers by using the summer survival estimates of adult females over a 28-day period to successfully predict population growth (r) for the entire year ($n=9$ consecutive years).

Methods

Study species

The arctic ground squirrel is a burrowing, semi-fossorial polygynous sciurid (McLean 1981) inhabiting arctic and subarctic regions of North America and Russia (Naughton 2012). They are typically found in open meadows and tundra, but one of the unique features of their geographic distribution is the extension of their range into the boreal forests of the Yukon and NW British Columbia. Squirrels hibernate for 7-9 months (September/October through April);

the remaining active-season is short and individuals must reproduce and gain substantial mass (energy reserve) during this time (Buck & Barnes 1999a). Juvenile squirrels are born in May but remain in the natal burrow for nearly one month before emerging (with females being philopatric and males dispersing) to establish a territory, and gain sufficient mass to survive winter hibernation (Carl 1971, Lacey 1991, Sheriff et al. 2013a).

In northern ecosystems, this common small mammal functions as an important prey item (Hubbs & Boonstra 1997), herbivore (Boonstra et al. 2001) and as an ecological engineer (Price 1971). Their distribution drives the abundance and spatial arrangement of other ecosystem constituents from carnivores to plant communities (Wheeler & Hik 2012). In the SW Yukon ground squirrels are an important alternate food source for mammalian and avian predators such as the coyote (*Canis latrans*), lynx (*Lynx lynx*), Northern goshawk (*Accipiter gentilis*) and Red-tailed hawk (*Buteo jamaicensis*) (Doyle & Smith 1994, O'Donoghue et al. 1998a,b).

Study area

The area is in the rain shadow of the St. Elias Mountains and receives a mean annual precipitation of ca. 230 mm, mostly falling as rain during the summer months, but including an average annual snowfall of about 100 cm (Krebs, Boutin & Boonstra 2001). Squirrel and hare data were collected on two 9-Ha trapping grids, located several kilometers apart (~900 m above sea level (asl)) (61°00'38"N, 138°11'31"W and 60°55'53"N, 137°58'25"W). These grids were dominated by white spruce forest (*Picea glauca*), willow (*Salix* spp.) or bog birch (*Betula glandulosa*) thickets, and occasional aspen stands (*Populus tremuloides*) (see Boonstra et al. 2001 for detailed trap locations and Turkington et al., 1998, 2002 for regional descriptions).

Population estimates

Squirrels and hares were trapped twice yearly (May and August) at two sites (GPC and Chitty grids; Boonstra et al. 2001) for 25 consecutive years (nearly 3 hare cycles; 1990-2015). The methods of data collection are fully described in Boonstra et al. (2001). Population density estimates were obtained by mark–recapture methods (described below). Each mark–recapture session consisted of between two (typically) or four (in situations of low AGS/hare density) consecutive days of trapping in May/August for AGS and April/October for hares.

Squirrels traps were set at 0800 h, checked every 1.5 h, and closed by 1230 h each trapping day. Arctic ground squirrels are highly trappable and recapture rates were high ($> 80\%$). Squirrels were live-trapped on two grids each with 50 traps spaced 30 m apart in a 10×10 pattern with traps placed at alternate grid stations. Live traps ($14 \text{ cm} \times 14 \text{ cm} \times 40 \text{ cm}$; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) were baited with peanut butter. Upon first capture, squirrels were transferred to a mesh bag, where they were then tagged in both ears with unique monel No. 1005-1 tags (National Band and Tag Co., Newport, Kentucky, USA), weighed (Pesola spring scale $\pm 5\text{g}$), sexed, and measured for structural size (zygomatic arch width) using a 150mm metric dial reading caliper. An index of relative abundance was derived for the period 1973-1989 by fitting the number of AGS counted per km of road along the Alaska highway [between Haines junction and the KLRS research station] to mark-recapture estimates from Kluane. These data were displayed graphically to corroborate the timing of peak cycles, but were not included in statistical analyses or computations of per capita population growth.

Snowshoe hare live-traps were pre-baited with alfalfa cubes for 3–5 days prior to being set. Trapping sessions consisted of 2–3 nights of trapping within a 5-day period in spring (early April) and autumn (October). The traps were set at 2200 hours and checked at 0600 hours to

minimise the length of time hares were detained. Upon capture, each hare was identified to sex, weighed with a Pesola spring scale (± 10 g), its right hind foot length was measured (as an index of body size), and its right ear was tagged (No. 3 Monel tags; National Band and Tag Co., Newport, Kentucky, USA). Trapping and handling protocols were approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council on Animal Care (NIAUT certificate # 5740 – 13) and all research was sanctioned under the Yukon Scientist and Explorers Research permit (License # 14-10S&E, file # 6800-20-43).

Statistical analysis

Population density and standard errors were estimated using a mark-recapture heterogeneity (jackknife) model (Pollock et al. 1990) from Program Capture (White et al. 1982, Rexstad and Burnham 1991). We calculated the effective sample area (to produce a density estimate) for each trapping period by adding a boundary strip to the edges of the trapping grid equal to half the mean maximum distance moved (Otis et al. 1978, Krebs et al. 2011). This method performs equally well to other density estimates for small mammals (Krebs et al. 2011). Rates of population increase were calculated for seasonal and annual time intervals. Yearly rates based on spring census data were used to generalise annual patterns of change over time. To distinguish between possible Type II and Type III predator relationships, the instantaneous rates of increase were calculated for each active-season (May-August). The shape of the predator prey relationship was determined by plotting the instantaneous per capita rate of change for AGS between N_t and N_{t+1} ($dN/dT/N_t$) over population density at N_t (Sinclair et al. 1998). Data from 1990 and 1999 were excluded from this plot because these years coincide with intense prey-switch events that result in total population collapse (such perturbation events are treated separately when analysing cyclic dynamics; Sinclair & Krebs 2002). Because the application of

goodness-of-fit curves to time series data is inappropriate, regression curves are used only to predict the regions where rates of change are zero. The slope of the regression curve where it crosses the zero line was used to classify stable equilibria and/or unstable boundaries.

All other statistical analyses were calculated using the programs JMP version 4.0 (SAS institute Inc., Cary, North Carolina, USA) or StatistiXL version 1.8. We measured correlation between hare and AGS densities for the time periods 1990-2011 and 2012-2014 by calculating the coefficient of determination using ordinary least squares regression. We used the Chow Test (Chow 1960) to test if the coefficients of linear regression for each time period were equal. This is used in the analysis of time series data to test for structural breaks in the correlation dynamic of a single explanatory variable (Chow 1960). Mann–Whitney U-tests were used to compare median population densities where data were not distributed normally.

Results

Both hare and ground squirrel population density were marked by repeated fluctuations (Figure 4.2) that were coincident between 1990-2001 ($R^2=0.69$; Figure 4.3) but not coincident between 2002-2013 ($R^2=0.01$; Figure 4.3). The amount of variation in squirrel density explained by hare density (R^2 value) differed significantly between the two time-periods (Chow Test: $F_{2,14}=33.4$, $p<0.001$; Figure 4.3). After 2000, the AGS population failed to increase despite a modest rise in hare numbers including peaks of hare abundance in 2005 and again in 2015. Mean density for the period preceding the year 2000 was significantly larger (by one order of magnitude) than for the interval following the pivotal population decline ($U=41$, $n_1=24$, $n_2=26$, $p<0.01$). Figure 4.4 illustrates two patterns: first, the annual rate of change for the decline phase of the hare cycle follows a different track from that for the increase (circular pattern to the right);

and second, the overall dynamic moves from visually circular to unstable below a threshold density of ~ 0.5 AGS individuals/ha (Figure 4.4).

To estimate the total predator response, the instantaneous rates of AGS per capita population growth for the active-season period (May-August) were plotted against spring population density. Over the entire range of densities recorded for AGS the density dependence relationship is curvilinear (Figure 4.5), and conforms to a Type II predator-prey relationship (Figure 4.1). The rate of population change crosses the zero line at two specific density locations. The upper stable point in Figure 4.5 is equivalent to point C in Figure 4.1; here density dependent processes act to maintain squirrel density at ~ 2 /ha, which is the historical carrying capacity (Werner et al. 2015a). The negative downward slope of the population function at point C is indicative of population regulation (Sibly and Hone 2002). In contrast, the lower threshold (~ 0.25 - 0.5 /Ha) is an unstable boundary below which AGS abundance can decline toward extirpation (Figure 4.5). Because density dependence varies from values which are weakly positive to negative, there is little compensation for stochastic effects at or near this threshold.

Discussion

Study limitations

Our aim is to infer the nature of the predator-prey relationship and to assess prospects for population recovery. A variety of *a priori* reasons exist to expect predation to show strong signals through the noise of contingent events in this part of the boreal forest (Boutin et al. 1995, Krebs et al. 2001, Donker & Krebs 2012, Werner et al. 2015b). However, the possible contribution of Allee Effects (Allee 1931) to the extinction process must first be considered. Social processes can cause per capita rates of change similar to those seen in Type II predator interactions, but without recourse to predation (Odum & Allee 1954). The range of mechanisms

that could contribute to Allee Effects for AGS include lower mate finding success (Stephens & Sutherland 1999), lowered reproduction resulting from poor body condition, reduced group vigilance and alarm calling (Stephens & Sutherland 1999), the loss of conspecific cues for habitat choice (Reed & Dobson 1993), and other forms of behavioural dysfunction (Brashares, Werner & Sinclair 2010).

Because the mating system of the arctic ground squirrel is polygynous, mate-finding limitation caused by skewed sex ratios at low population size is not likely to cause inverse density dependence. It has been shown that adult females from this population over the same time period were in good hibernating condition by autumn (Werner et al. 2015b) and, because these females hibernate singly, their reproductive output the following spring cannot be attributed to any socially-mediated or density related process prejudicial to reproduction. Conspecific attraction may play a role in low rates of recolonization but this process will not hasten population decline because resident females are philopatric (Carl 1971) and site abandonment has never been observed (S. Donker, R. Boonstra, pers. comm.). However, the lost benefits of predator detection and signalling behaviour common to ground squirrels (Sherman 1977) and other social rodents (Blumstein 2007) at low numbers remains a possible contributing factor. Be it noted however that although Allee effects may aggravate population declines and/or constrain population recovery, they are inadequate to trigger such a decline (i.e., operate at low density).

It has been shown theoretically (Holt 1977) and empirically (Pech et al. 1995) that when the abundance of primary prey increases, the attendant increase in predators results in a decline in the abundance of secondary prey. However, when the preferred prey undergoes dramatic cycling, shifting predator preferences at different phases in this cycle can result in similar timing

of fluctuations and coincident declines in the abundance of secondary prey (Norrdahl & Korpimäki 2000). The strongly asymmetrical nature of indirect effects purported here (changes in hare abundance cause similar changes in ground squirrel but not vice versa) precludes using AGS extirpations as a natural test of these indirect effects. Only the removal of hares could serve as such a test. However, the large and nearly simultaneous fluctuations in numbers of both species (Figure 4.2) coupled with the observation that ground squirrels do not cycle in the absence of hares (Donker & Krebs 2011) provide compelling evidence for the existence of these indirect interactions up until 2000. Further evidence for the role of predator-induced indirect effects for synchronising population oscillations of these sympatric prey species come from i) detailed studies linking AGS cycles to intensified predation during their decline phase (Hubbs & Boonstra 1997, Byrom et al. 2000), and ii) the observation that the density, hunting behaviour, and diet of these same predators alter predictably with hare abundance (O'Donoghue et al. 1997, 1998a, 1998b).

Depensatory predation is possible in multi-prey systems where predators persist irrespective of secondary prey abundance (Holt & Lawton 1994). Where a curvilinear (hump-shaped) density response exists, stochastic population losses are not compensated for by positive density dependent processes at low population size. In such cases of inverse density dependence populations below a certain threshold will trend to extinction (Sinclair & Krebs 2002). Here we demonstrate a type II predator-prey relationship and quantify the critical density threshold ($>0.7/\text{ha}$) necessary for the persistence of AGS in the Yukon boreal forest system where hares are the preferred prey species for a range of predators (O'Donoghue et al. 1998a). The breach of this lower boundary during 1999-2000 is the most likely explanation for the loss of the alternating indirect relationship with the snowshoe hare, and for subsequent loss of cyclicity in

AGS abundance. These findings indicate that, as a secondary prey species, AGS may succumb to compensatory mortality from predators that are otherwise sustained by an abundant primary prey (DeCesare et al. 2010). The existence of prey switching during specific periods of the hare cycle further exacerbates this unstable dynamic by reducing the length of time squirrels remain at or near carrying capacity.

Upon first inspection, the decade long persistence of ground squirrel numbers at very low densities appears to corroborate a lower stable equilibrium characteristic of a type III predator interaction (Figure 4.2). Inspections of this annual time series prompted Werner et al. (2015a) to hypothesize the possible existence of predator regulation of prey at low prey numbers. However, when changes to population density are limited to marked individuals caught at the beginning and the end of each active-season, we find that the local population sometimes dropped to zero in autumn, only to exhibit positive numbers the following spring. The existence of multiple extirpation events on the same trapping grids were effectively obscured in yearly census data because unmarked dispersing immigrants settled into the newly vacant habitat (Donker & Krebs 2012). This discrepancy underscores the important fact that the resolution of population census data (annual vs. seasonal) must be fitted to the needs imposed by the research question. In this case it was important to estimate the per-capita rate of change by restricting our analysis to rates of change for the active-season only.

Because density dependent relationships are notorious for their non-repeatable characteristics over time and space (Krebs 2002) the patterns we report may have limited wider application. However, given widespread concomitant disappearance of AGS from boreal forests in Kluane (Gillis et al. 2005a, Donker & Krebs 2011) and much of the low elevation habitats of the southern Yukon (Werner et al. 2015b), an intensification of predation across large areas may

be a contributing factor. For example, the most recent surveys of Lynx abundance for this area indicated that during the last low phase of the hare cycle (2008-2012) Lynx were more numerous than ever recorded for any previous low (Krebs et al. 2016). In Kluane Lynx focus on alternative prey like red squirrels (O'Donoghue et al. 1998a) during the winter months in years when hares are sparse. Higher predator abundance in advance of the increase phase of the hare cycle (Krebs et al. 2016) makes future positive indirect effects between hares and ground squirrels less likely because of the shortened lag in the predators' numerical response to increased hare numbers.

The ultimate causes, however, for both the breakdown of population cycles in northern regions and for the observed shifts in prey abundances reported here are probably being driven by larger ecosystem changes. The dampening of cycles is being reported throughout the circumpolar sub-arctic. For example, cycles in voles and forest grouse in Europe and Lemmings in North America are breaking down; in both cases climatic forcing is considered the likely underlying cause (Ims et al. 2008, Reid et al. 2012).

We propose that predation, being the most consistent explanation for this documented population collapse, is the *most likely proximate cause* of local ground squirrel extirpation from the Kluane boreal forest monitoring grids. The principle assertions of this paper – the existence of Type II predation and an unstable critical threshold in prey density – are being tested by raising the local density of AGS above 0.7 / ha in a series of experimental reintroductions into formerly occupied habitats within the boreal forest zone (Werner 2015). This study offers a practical example of how monitoring per-capita rates of change can be used to infer regions of population attraction and thresholds of instability and, by extension, the range of prey densities where persistence is most likely.

Tables and Figures

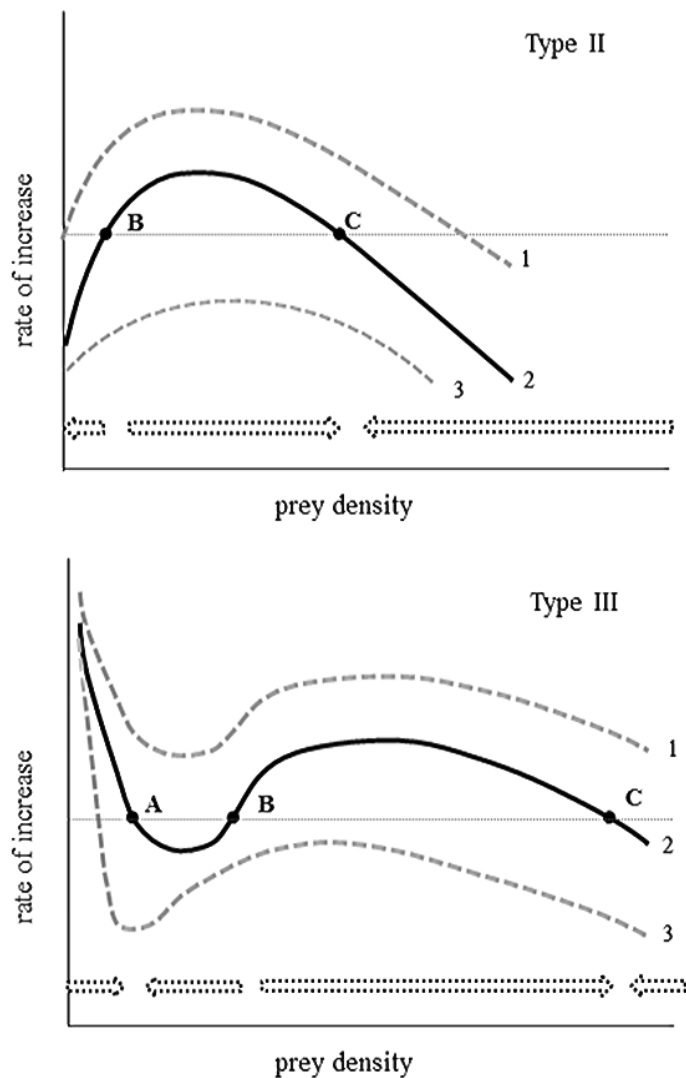


Figure 4.1 An illustration of the instantaneous rate of change for a prey population experiencing varying levels of Type II and Type III predation. Arrows represent direction of projected population change relative to stable equilibria (a, c) and an unstable boundary threshold (b). Curves 1 and 3 represent different levels of predation rate (1 = lowest; 3 = highest). Key distinguishing features for a Type II is for declining prey population growth at low prey density, but for Type III a lower stable equilibria results from positive population growth at low numbers. Adapted from Sinclair and Krebs (2002).

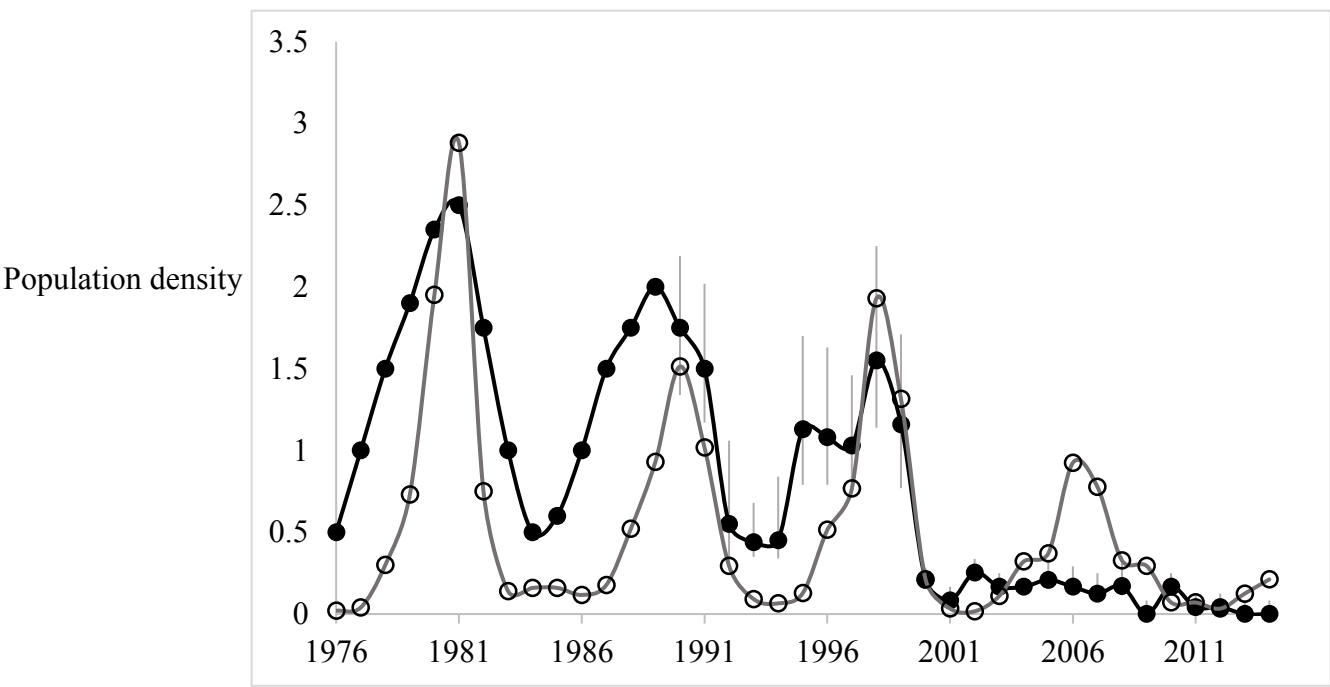


Figure 4.2 Changes in the spring density of arctic ground squirrels in two live-trapping grids in the boreal forest at Kluane Lake since 1977 (filled circles) and the spring density of snowshoe hares in the same habitat (open circles). Data from Werner et al. 2015; AGS density estimates for 1977-1989 are based on an index of abundance, while 1990-2015 are mark-recapture estimates. Grey vertical bars are 95% confidence limits.

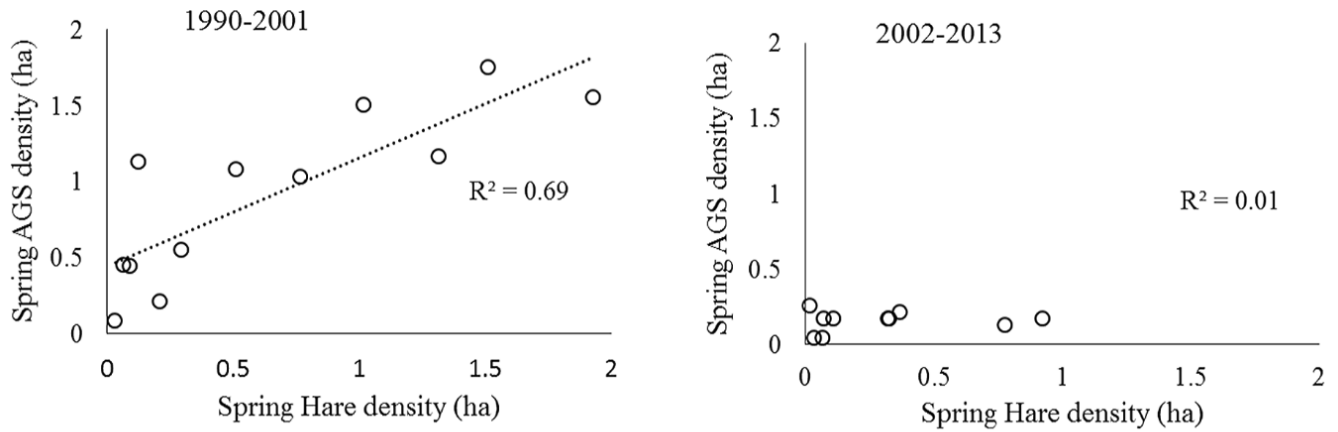


Figure 4.3 The historical relationship between spring density of sympatric populations of snowshoe hare and arctic ground squirrels in the boreal forests of the Kluane region, SW Yukon. The time periods represent conditions before and after the population collapse of ground squirrels. A high correlation is consistent a preference by predators for hares, and of prey-switching among predators from hares to AGS during the decline phases of the hare cycle.

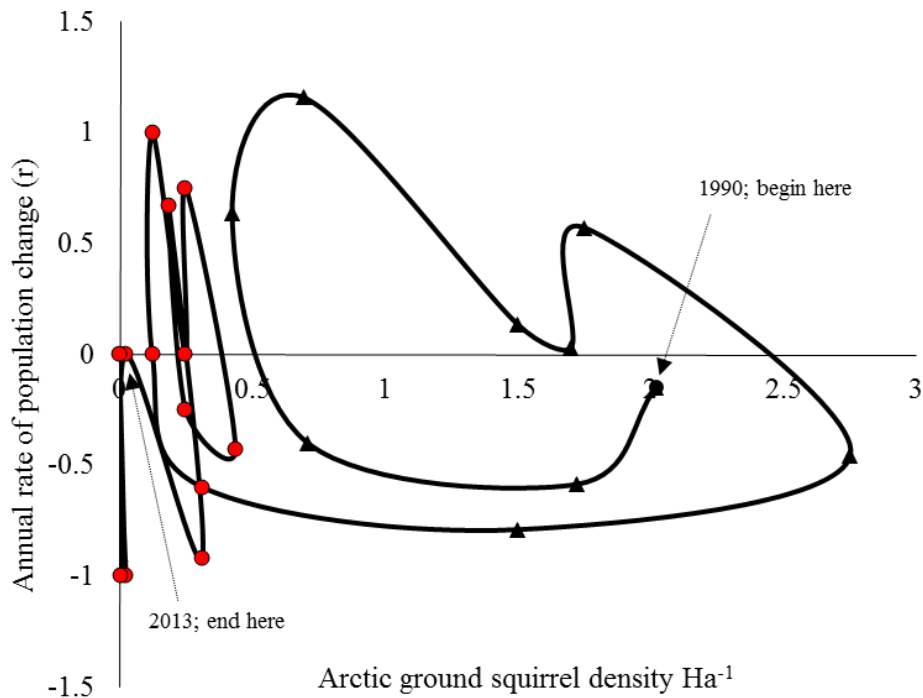


Figure 4.4 Rate of increase (r) for arctic ground squirrels in relation to its population density between 1990-2013 (annual spring trapping records; Kluane, SW Yukon). The data comprise one cycle and subsequent non-cyclic dynamics post 2000. The rate of AGS increase follows a different path from that of the increase phase, due the periodic intensification and relaxation of predation resulting from predator preference for the snowshoe hare (first 10 data points). The rates exhibit unstable dynamics below a density threshold of 0.5/ha, that end in eventual localised extinction (final 13 data points).

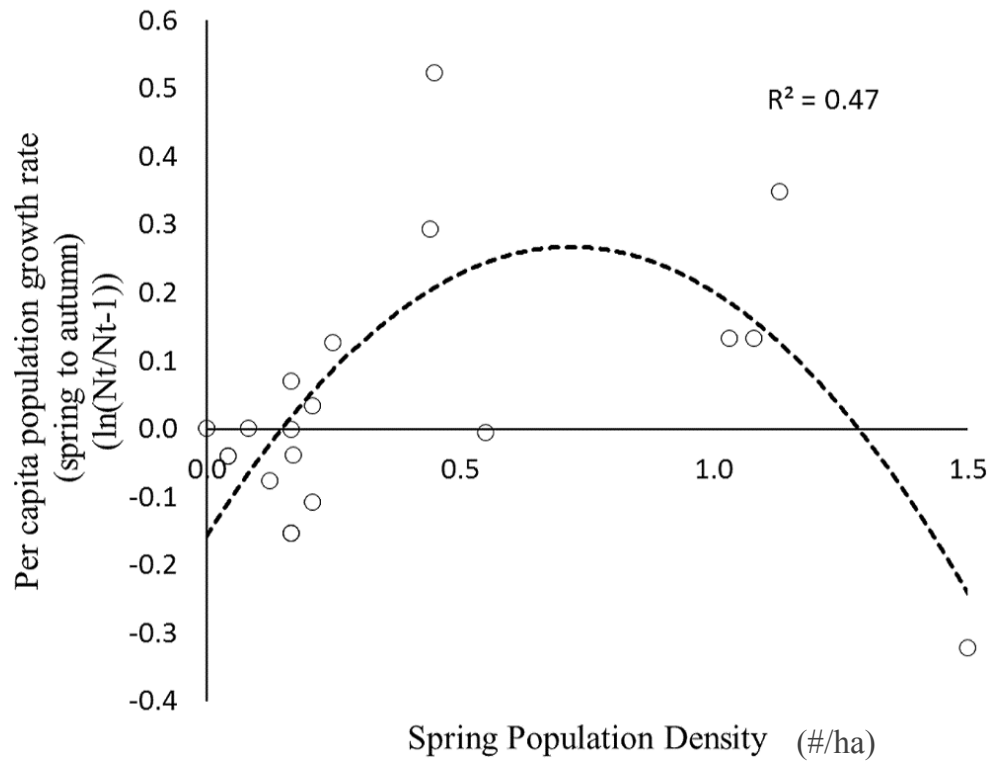


Figure 4.5 The instantaneous rate of population increase for the arctic ground squirrel during the non-hibernation period (May—August) plotted against spring population density 1990-2013. This hump-shaped relationship is indicative of inverse density dependence at low population density.

Chapter 5: Factors affecting the distribution of the arctic ground squirrel in the southern Yukon - an occupancy analysis

The following chapter is presently being submitted to the Journal of Animal Ecology (September 2016).

Introduction

Northern terrestrial ecosystems are in a profound state of flux (Epstein et al. 2004, Henry et al. 2012) as are the factors controlling the abundance and distribution of resident wildlife (Ozgul et al. 2010, Elmhagen et al. 2015). Spatial transitions in the environmental controls of vegetation patterns, ecotones, and animal distribution are of particular interest in Canada's montane, boreal and arctic environments (Wheeler et al. 2015). The extent to which herbivores will tolerate these environmental impacts will vary, as will the strength and nature of these impacts across a species latitudinal range (Hersteinsson & Macdonald 1992, Post & Forchhammer 2008). Even the most basic qualitative predictions concerning the direction of population response to environmental change requires some knowledge of the class of factors to which populations are most sensitive (Krebs 2002, Legagneux et al. 2012).

In particular, whether small herbivores are predicted to benefit or suffer from projected environmental alteration will depend upon their current form of population limitation and regulation (e.g., Hersteinsson & Macdonald 1992, Madsen et al. 2011). Whereas increases in primary productivity will favor species limited by energetic constraints (associated with food shortage or harsh winter conditions), species that routinely endure intense predation will be particularly affected by changes to the total response of predators (Sinclair & Krebs 2002,

Elmhagen et al. 2015, Werner et al. 2016). An intriguing and under-investigated issue concerns what specific biotic and abiotic features of habitats influence the processes of extinction.

Here I evaluate a suite of fine scale habitat components to explain localised extinctions of an important colonial herbivore, the arctic ground squirrel (*Urocitellus parryii*; AGS), throughout its southern range. To achieve this, I measured the association between colony status (extinct vs. extant) and the relevant biotic and abiotic features previously identified in the literature as exerting an influence on ground squirrel reproduction and survival.

I constrained the scope of study, via intensive sampling, to confirmed colony sites identified by the presence of burrows, and thus known to have supported AGS in the recent past (~15 years; Boonstra pers. comm.). Because each colony may be assigned as “extant” or “extinct” with a high degree of certainty, the usual complications of how to interpret the biological significance of species absence in many occupancy studies are avoided (Gu & Swihart 2004, Mackenzie et al. 2005). This study reports on the most comprehensive survey of colony occupancy yet conducted for this species.

Methods

Study species

The arctic ground squirrel is a semi-fossorial (burrowing) holarctic rodent common to arctic and northern montane boreal ecosystems. They are the most northerly distributed squirrel in North America (Naughton 2012) and are considered a generalist herbivore that consumes a variety of forbs and grasses (Batzli & Sobaski 1980). As an adaptation to harsh winter conditions, this small mammal hibernates for 7-9 months each year (August/September—April) (Sheriff et al. 2011). Females breed within days of spring emergence (mid-April) (Buck & Barnes 1999a, Sheriff et al. 2015) and produce a single litter ~25 days later (mid-May) (Green

1977, Lacey, Wieczorek & Tucker 1997). Juveniles are weaned and emerge from their natal burrow in mid/late June. Nearly all males disperse, whereas females settle within their natal home range (mean dispersal distance for males and females was 515m vs. 120m; Byrom & Krebs 1999). In arctic and subarctic regions, they form permanent social colonies comprising shallow underground burrow systems (~1m depth) which provide refuge from predators and thermal stress, and are used for maternal denning and overwinter hibernation (Carl 1971, McLean & Towns 1981). These burrow systems may last for decades after colony extinction (Werner et al. 2015a); the persistent nature of these burrows is a key feature for this study. Throughout the southern Yukon (Canada) AGS occupy small clearings within boreal forest, low to mid-elevation meadows, and alpine.

Arctic ground squirrels are a seasonally important food source for falcons, owls, hawks, Canada lynx, coyotes, foxes, wolves, and grizzly bears (Carl 1971, Boonstra et al. 2001, Gillis et al. 2005, Donker & Krebs 2011). They are also hunted by Yukon First Nations as a traditional source of food. Population fluctuations of AGS therefore regularly affect the food supply available to these predators.

Population control in arctic ground squirrels has been hypothesized, in various contexts, to be driven by diverse factors such as sociality (Carl 1971), food (Carl 1971, Batzli & Sobaski 1980), and overwinter severity (Karels 2000), and predation (Hik et al. 2001, Donker & Krebs 2011, 2012, Werner et al. 2015a).

Study area and occupancy Index

Grounds squirrels were found in four distinct habitats in the SW Yukon (Figure 5.1) – low-elevation meadows, clearings in the boreal forest, mid-elevation meadows, and alpine. Low meadows are typically scattered within a matrix of forest that range in elevation from

approximately 500 to 1000m asl. Many of these meadows are associated with steep south-facing eskers, historical fires, river banks, or old flood plains of glacially fed rivers. Colonies in the boreal forest habitats are primarily under canopy gaps and small shrub-dominated clearings. Mid-elevation meadows (1000-1500m) are surrounded by coniferous forest (overstory being a mix of *Picea glauca*, *Pinus contorta*, and *Betula* spp.) and deciduous forest (primarily *Populus tremuloides*), or by thick shrub (*Salix* and *Betula* spp.) that range from 40 cm to several meters in stature. In contiguous alpine (1500m-2200m), tundra forms the dominant landscape, with isolated shrub islands and variable topography influencing visibility at each site. Vegetation in all habitats comprised mainly graminoids, with proportions of forbs, bryophytes and lichens varying between sites. Low meadows associated with pasture, agriculture and other anthropogenic influences were excluded because I considered those habitats to be outside the purview of some of the covariates in our study (Werner et al. 2015a).

To obtain a landscape data set on the distribution of ground squirrels in all available habitats, from the forest to the alpine, I determined the occupancy status of 221 populations over a 25,000 km² area during 2013 and 2014 (Figure 5.1). I later sub-sampled 138 colonies for inclusion in the analysis (see analysis section) to ensure each of the four habitat types contributed an equal number of extinct and extant colony sites. This subsampling corrected for the effect of habitat area (i.e., relative coverage over the landscape) and allowed for a balanced design, permitting me to address possible fine scale features of each colony that were related to population persistence. At the time of publication, data for the boreal forest (the most extensive habitat spatially) was excluded because too few extant sites currently exist (see Werner et al. 2015a for a discussion of this population collapse). This resulted in 48 low-elevation meadows, 44 mid-elevation meadows, and 46 alpine habitats; Figure 5.1). The minimum distance between

sampled colonies was set to 2 km as this value exceeds typical AGS dispersal distance (Byrom & Krebs 1999). Colonies were located by walking transects (800m - 3km, stratified by habitat) randomly placed overtop of high resolution orthorectified IKONOS satellite imagery.

To ascertain colony occupancy, I used a powder tracking methodology first developed for lemmings and voles by Boonstra et al. (1992) but adapted for AGS (Hubbs et al. 2000, Werner et al. 2015a). Small (5 cm × 7 cm) black plastic tiles (mean=71.6 SD=39.8) were placed in all burrows in a specified area (typically an entire colony) and left for six hours. The tiles were covered lightly in paraffin-based oil and unscented talcum powder. During retrieval if the tile was moved, covered in soil and showed tracks, the burrow was considered active. The area of each site indexed was obtained by recording the GPS coordinates of the corners of the site and then using MapSource (Garmin Corporation, Olathe, Kansas, USA; <http://www8.garmin.com/>, accessed 20 November 2014) to estimate the area in hectares (see Donker & Krebs 2011 for details). The area estimate was later used to calculate total burrows/ha. In the event of a discrepancy between the number of tiles deployed and the number of tiles retrieved, the number of tiles deployed was used in the calculation of burrow density and the number of tiles retrieved was used to determine the density of active burrows. Because AGS activity is influenced by both time of day and weather (Folk 1963), indexing was conducted between 0800 and 1600 during clear weather conditions.

Arctic ground squirrels are highly active during the day and powder tracking provides an effective method to determine the activity status of a single burrow (Hubbs et al. 2000, Donker & Krebs 2011) and the occupancy status of a colony with near perfect accuracy. The composite probability of non-detection for an entire colony can be expressed as:

$$P_{(\text{non-detect})} = [1 - P_{(\text{detect})}]^n$$

where $P_{(\text{detect})}$ is the probability of detection using powder tracking, and n is the true number of active burrows. Even with a very low detection probability at individual burrows (e.g. 0.5), the overall chance of failing to classify a colony as active is vanishingly small—except in extreme low density cases (1 or 2 individuals per colony) where stochastic processes make imminent extirpation likely. By employing this powder track technique, we circumvent the ostensible effectiveness of ascribing burrow activity by the interpretations of “signs” such as recent digging or feces. Tracks made on the tiles by ground squirrels are readily distinguished from those made by any other burrowing species.

Landscape Measurements

I estimated i) plant species richness and plant abundance by forage type (as a means of assessing the quality and quantity of available food) ii) elevation and aspect (assumed to indicate environmental harshness), iii) soil textures (as an indication of susceptibility to early spring flooding), and iv) depth to permafrost or other barriers to burrow excavation (for its implication for hibernacula quality) (see Table 5.1 for a complete list and supporting references). I quantified the following additional parameters of i) visibility and proximity to visual obstructions (as these factors will modify threat detection), ii) slope angle (as influencing both flood risk and mobility; see Table 5.1). The methods used to assess these characteristics for each surveyed colony are described below under the rubrics vegetation, burrow characteristics, and environment parameters.

A. Vegetation

To identify species and abundance of food plants the vertical canopy projection of vegetation from the ground as viewed from above (approximate height=1.5m) was estimated visually (i.e., percent cover; Daubenmire 1959) for shrubs, grasses, forbs, and trees within

100x150 cm randomly located quadrats within each colony. Cover estimates were chosen because they allow for the rapid accurate assessment of vegetation (Bråkenhielm & Qinghong 1995) and because they equalize the contribution of species that are very small, but abundant, and species that are very large, but few. The number of sample quadrats was determined by plotting, in the field, the saturating curve of cumulative species richness over plot number (Cain 1938). Sampling effort was terminated when the slope of this line approached zero (mean plot number=7, range=4-14).

To minimise observer bias, one dedicated observer completed all vegetation measurements (J. Werner) at every colony. To aid in cover estimations, quadrat plots were further divided into four 50x75cm sections (Sykes, Horril & Mountford 1983). Standard comparison charts (Terry & Chilingar 1955) and pieces of cardboard of known cover value (1, 5, 10, and 25%) were used as references during the estimation of foliage cover. After measurement, the top layers were sometimes removed to ensure understory layers were properly estimated. Vegetation sampling was constrained to the approximate dates of peak vegetation abundance (July 1-20; Turkington, John & Dale 2001). Plants were identified to species using Cody (2000) and pressed specimens were preserved for future reference.

B. Burrow characteristics

A single composite soil sample (~500 ML) was obtained by combining samples from the porch material (dirt mounds immediately below a burrow entrance) of at least 10 randomly selected burrow complexes within each colony. Coarse fragments were removed from dry samples using an 8" diameter ASTM 2mm mesh sieve. The percent sand (particle diameter=0.05-2mm), silt (0.002-0.05mm) and clay (<0.002mm) of each sample was determined by their settling rates in an aqueous solution, using a hydrometer (accurate to $\pm 2\%$; ASTM

2000). Soil particle size distributions sum to 100, and their relative compositions determine soil porosity (Hazan 1892, Fraser 1935). Maximum possible burrowing depth was determined by measuring the distance from ground surface to permafrost or bedrock using a 1.2m graduated stainless steel rod (AMS one-piece probe; accurate to ± 1 cm). The rod was inserted into the ground to the point of resistance in 20 random locations within every colony. A distinctive sound and feel is apparent when ice-rich frozen ground is met, and this was noted when encountered. Burrowing depth was recorded as >120cm if restrictive horizons were not detected before the probe was fully inserted.

C. Environmental parameters

Mean slope was calculated using four measurements of the vertical angle (in degrees) between two parallel identical rods placed 30m apart up and down slope. Measurements were spaced evenly across the sample area and were obtained using a hand-held electronic clinometer (Haglöf EC II). Aspect (slope direction) was measured at five random locations by taking a compass bearing directly downhill. Aspect range was calculated as the greatest difference between any two opposing slopes. Elevation was recorded from the approximate centre of each colony using a portable GPS (Garmin Map62) accurate to ± 4 m.

Distance to nearest shrub or forest ecotone (>1m in height) was estimated using a range finder (Leica DISTO E7500i), as the number of metres from colony center to an ecotone of continuous vegetation greater than 2 m in height. Colony dimensions were also measured using a range finder. Visibility was assessed by observing the mean percent visible of a 1 x 1 m board (checkered into 100 squares) from a height of 20 cm above the ground (height of an AGS in alert posture; Sheriff et al. 2012). These visibility measurements were taken at each of the four cardinal directions at 5, 10, 15, 25, and 50 m from the four corners and the center of each site.

An additional index of incident solar radiation was calculated for each colony, using the equations developed by McCune & Keon (2002). Our motivation here was to provide an overall picture of potential energy used by plants and absorbed by snow in case more direct instantaneous measurements fail to capture the influence of sunlight on colony persistence. Input variables for the McCune and Keon (2002) equations are latitude, slope, and aspect. This index reflects the cumulative yearly solar energy at that location, including the prolonged period where AGS are hibernating underground.

Analysis

All variables were treated as continuous except distance to shrub/tree cover exceeding a maximum threshold, and soil depths exceeding measurement depths. A threshold in the relationship between distance to shrub/tree cover and extinction status was identified by graphical inspection, and an additional binary category was derived to reflect whether a colony was less than or greater than 100m from a shrub or forest ecotone. Soil depth greater than 120cm was also treated as a binary categorical variable. Aspect is a polar coordinate containing a radius (r) and a polar angle (t). The circular nature of polar coordinates presents a problem for their interpretation as continuous variables (e.g., the absolute difference in magnetic angle between 0 and 359 is far less than 0 and 10). To overcome this circularity, I converted aspect to a Cartesian coordinate system x, y by using the trigonometric functions $x = r \cos t$, and $y = r \sin t$, where t is an arbitrary constant.

Modelling procedures

The occupancy/extinction status of colonies was modelled using a case-control design (Song & Chung 2010) with a logistic regression model in the R command program glm.nb from

the MASS package (R Core Team 2015). The log-odds coefficients for each of the independent variables were weighted to account for collinearity (Grömping 2007).

All possible model combinations were computed for up to 7 variables of complexity, which is well within the 10:1 rule of thumb for subjects to predictor (Grueber et al. 2011). This yields over 400 000 unique model combinations. I sorted the models using the Akaike Information Criterion with an adjustment for small sample size (AIC_c; Burnham and Anderson 2004). This estimate, which amounts to the AIC value of a model with the addition of an extra penalty for number of parameters, is computed using the following formula:

$$AIC_c = AIC + \frac{2k(k + 1)}{n - k - 1}$$

Where n denotes the sample size and k the number of model parameters.

Each model was ranked relative to its proximity to that model with the lowest AIC_c value (i.e., the ‘top model’; Burnham & Anderson 2002) using the AICcmodavg package in R. Rather than focus on the single ‘best’ model selected from all possible model combinations, inferences were instead drawn from the entire set of models not larger than 2 AIC_c from that model ranked with the lowest AIC_c value (Burnham & Anderson 2004). This yielded a top set of 10 models, and 15 unique predictors (Table 5.2). During the model generation phase an unworkable degree of collinearity was discovered between aspect and elevation, and the derived values of incoming solar radiation (McCone & Keon 2002) when models containing these variables failed to converge. Because this index, which is partially derived from measured variables, risks redundancy with those measured variables it was removed at this point from the global parameter set (Bolker 2009). Similarly, the clay-silt-sand categories, which sum to 100%, necessitated that one variable be arbitrarily removed. Because the estimates for %silt and %sand were both

positive but that for %clay negative, clay content was removed. The explanatory significance of the sand and silt variables should therefore be considered within this context.

Model averaging procedures

Model averaging was completed using the MuMin package in R. It computes the Akaike weights for each of the 10 top models and then computes a weighted averaged for each predictor variable (Barton 2011). The results of the model averaging are summarised in Table 5.3. A measure of the precision of each model-averaged estimate was obtained by computing unconditional standard errors (Burnham & Anderson 2002). These parameter coefficients are the standardized effect sizes and are therefore on a comparable scale (Grueber et al. 2011). For ease of interpretation the relative importance of each predictor was computed as the sum of the Akaike weights of the models which include that predictor (Barton 2011).

The coefficients for a continuous predictor represent the log odds associated with a one-unit change in the predictor. The coefficients for categorical predictors are the log odds between that category and the reference category. The model averaged logit coefficients (un-standardized) were exponentiated in order to compare the ratios of the probability of occupancy to that of extinction associated with a one-unit change in each predictor variable (odds ratios). Confidence intervals for the odds ratios were obtained by first calculating the end points of the confidence interval for the log odds, then converting these values. These odds ratios are a more intuitive measure of the association between the predictor and outcome variables, and their interpretation does not depend on the level of the other variables in the averaged model.

Results

On average both extinct and extant AGS colonies are relatively small (<1 ha in size) and are situated on sparsely vegetated (31% ground surface containing no plants) moderate slopes (~20°) containing loamy sand soils (79% sand, 18% silt, 3% clay) with deep unconsolidated parent material (exceeding 1.2m). Most colonies consisted of a dense aggregation of burrows (~400/ha). Visibility from these vantage points was greatest at close proximity (5m=86%, 10m=70%) and generally decreased with increasing distance (mean visibility=52, 37, and 18% at 15, 25 and 50m respectively).

In terms of predicting the occupancy of colonies observed in this study, the percent sand in burrowing matrix, the soil depth and visibility at a distance of 50m were the most important factors correlating to squirrel presence (relative importance=1.0; Table 5.3). The hillslope angle, forb species richness, and the percent of the colony area containing no plant cover were also relatively important (97%, 91%, and 91% respectively), with the remaining parameters ranged in importance from 7% (% shrub cover and visibility at distance of 5 and 15m) to 18% (visibility at 10m). All parameters with high relative importance (>0.8) also exhibit 90% confidence intervals that do not overlap with 1 (Table 5.3); however, at the 95% level only visibility at the furthest range of measurement (50 m) retains certainty in its positive relationship to colony persistence (Table 5.3).

Model averaged parameter estimates indicate that the odds of occupancy increase by a factor of nearly 10% with each additional percent increase in the proportion of sand in the burrowing material (Figure 5.2). An incremental addition to silt content also resulted in a small (1%) but positive benefit. Every 1 cm of soil depth yields (up to a maximum of 1.2m) a 9.6%

positive change in the odds ratio, and if soil depths exceed 120cm there is a further 63% greater odds of colony persistence (Figure 5.2).

In contrast, a 1% increase in the coverage of bare ground results in a nearly 7% reduction in the odds ratio of occupancy to extinction. Raising the amount of shrub cover also has a marginally negative result (~0.1%) for colony persistence, although the sign of this term is uncertain. Increases to forb richness, however, have a strong positive influence (relative importance=0.91; Table 5.3) and for each additional forb species present the odds of colony occupation increase by 6% (Figure 5.2).

A 1% change in visibility over a 50m interval results in a 14% change in the odds that a colony will be active, while conditions across shorter distances result in 0.1-0.2% change in the odds of occupancy. A one-unit change to slope angle and colony area shift the odds of occupation by 13% and 9%, respectively. Increases to elevation result in a marginal negative % change to the odds that a colony will be active (Figure 5.2).

Discussion

Here I explore several non-exclusive hypotheses accounting for large-scale patterns of persistence throughout the southern Yukon. Explanatory variables commonly linked to food quality and quantity, soil and burrowing quality, and threat detection appear to be important indicators of extinction risk (Table 5.3). I discuss significant components of the top model set in terms of the plausible mechanisms which maintain these statistical associations.

Soil constituents

The risk of catastrophic flooding of burrow systems will decrease as the permeable characteristics of the surrounding soils increase. This, in turn, will be influenced by the distribution of soil grain sizes (Fraser 1935). Soil containing larger fractions of sand or silt will

drain more rapidly than soils with lesser porosity. In addition to ameliorating flood risk, burrow materials high in sand or silt probably require less energy to excavate. Given the extinction context of this study, the explanatory importance of soil texture is best considered in terms of flood potential. Other ground squirrel species that survive much wetter climates build complex drainage channels to draw flood waters away from their hibernation chamber (e.g. Shaw 1926, King 1955). The architecture of AGS hibernacula have never been described. However, while excavating four hibernacula during September 2015 for purposes of retrieving dropped radio collars I observed no drainage holes associated with any of the observed chambers. Whereas the gradual loss of digging behaviour associated with drainage architecture would result in energy savings during the dry glacial periods in Nearctic Beringia (Eddingsaas et al. 2004), the contemporary lack of drainage may now result in greater susceptibility to spring rain-on-snow events; the frequency and severity of these events appear to be increasing in the southern Yukon (Donker & Krebs unpubl. data).

Soil depth

The model averaged coefficients for soil depth within the measurable range of 120cm and for soils exceeding this depth indicate a positive relationship between maximum burrowing depth and the odds of colony persistence. Deeper burrow systems provide maximal thermoregulation by avoiding areas with shallow permafrost and by protecting hibernating animals from low winter temperatures above ground (Buck & Barnes 1999b). Hibernacula chambers which are located at greater depths are also more likely to be insulated from the type of spring rain-on-snow events observed during years of population decline in the Kluane region (Werner et al. 2015a).

Bare ground cover

A positive association between the area of a colony not in food production and its risk of extinction suggests that food scarcity interacts with other threatening processes, as has been previously observed for this species (Hubbs & Boonstra 1997, Byrom et al. 2000). Small population sizes are also naturally more susceptible to stochastic variation in demographic or environmental parameters. Many of the sparsely vegetated colony sites were either in very dry valley bottom micro climates where soils are dominated by cryptogammic crusts, or at high elevations where unstable scree and shale deposits routinely covered vegetation. Future study correlating forage with population density, coupled with experimental exclusion of ground squirrel herbivory, would serve to clarify the mechanism behind this observation.

Food acquisition and escape are often considered as mutual costs, expressed by the opposing activities of foraging and risk management (Lima & Dill 1990). In this context, food scarcity may increase one's vulnerability to predation by forcing an individual to feed further from safety or to invest less time in vigilant behaviour. An interaction between food availability and predator abundance for influencing population growth rate has been experimentally confirmed for AGS in boreal forest habitat of this region (Hubbs & Boonstra 1997, Krebs et al. 2001).

Plant metrics

Forbs are among the most important food plants for arctic ground squirrels (Batzli & Sobaski 1990). Increased forb richness will benefit ground squirrels in that multiple plant species increases the variety of species-specific phenologies at that site, which may prolong the period of available forage. Alpine plants also contain a great number of secondary compounds (Jung et al. 1979) whose digestible and nutritional value for squirrels are poorly understood (Werner 2012).

The negative association between colony persistence and shrub abundance suggests that present and future shrub expansion may result in range contraction of AGS regions where these ecotones are advancing. However, as other studies on the influence of shrubs on AGS demonstrate, the interactions between shrubs and food, shrubs and micro-climate, and shrubs and active-season mortality are likely to interact in complex ways that obfuscate generalisation (Wheeler & Hik 2014a,b, Wheeler et al. 2015).

Slope angle

Steeper slopes may serve both as physical protection and a factor enhancing drainage. The importance of slope to drainage will depend upon the colony's meso-slope position (water shedding hill crest vs. low lying depression; Beever & Belant 2011) and the regional moisture regime. However, a positive relationship between slope and an index of population density (see Hubbs et al. 2000) was recorded during a 2012 pilot study ($r^2=0.72$, $n=32$, unpubl. data) in the dry-belt of the S.W. Yukon. These sites are on xeric southwest-facing slopes under strong influence of chinook winds that preclude snow accumulation and, therefore, any possibility of catastrophic flooding. Slope must therefore confer other benefits to ground squirrels in addition to reducing flood risk.

The slope angle on which a colony is situated will strongly influence the speed and mobility of terrestrial predators and, to a lesser extent, the attack success of avian predators (Blumstein et al. 2004). Many northern herbivores occupy steep or otherwise unnavigable habitats for at least part of their life history (e.g., marmots; Allainé et al. 1994, Barash 1989, and pikas; Franken & Hik 2004). Marmots are less vigilant when foraging on steeper slopes, likely because risk of predation is lower in these environments (Blumstein et al. 2004). For arctic ground squirrels living under periodically heightened predation, steep areas appear to constitute

beneficial habitat, to the extent that such habitats were used successfully to predict the spatial distribution of mortality (Karels & Boonstra 1999). Here I report slope angle as an important explanatory factor in colony persistence; similar slope-persistence relationships are reported for yellow-bellied marmots in Colorado (Blumstein et al. 2006) but, as with this study, the mechanism driving this relationship are unclear.

Elevation

Gillis et al. (2005a) reported that annual survival of AGS did not vary with elevation, but instead noted a trade-off between active-season and overwinter survival. In this study a weak but significant negative relationship was found between occupancy and elevation (Figure 5.2 & Table 5.3). This is surprising, it is generally expected that equilibrium densities of this species are greater at higher elevations (Green 1977, Donker & Krebs 2012). In addition, predation is at least periodically more intense at lower elevation, owing to prey switching between AGS and snowshoe hares (Boutin et al. 1995, Byrom et al. 2000, Werner et al. 2016), which should increase extinction risk at these locales. However, where other contingent factors are held constant, the adiabatic cooling of a dry parcel of air is approximately 1°C for every 100m increase in elevation. Colonies in high mountain terrain will experience cooler climates and shorter subsequent growing seasons than populations situated in valley bottom habitats. Sheriff et al. (2012) found that AGS living at higher elevations had greater stress hormone levels, a condition which has been associated with reduced reproduction. Similar negative associations between survival and elevation exist for yellow-bellied marmots (Ozgul et al. 2006). It is possible that increased environmental harshness associated with mountain-top environments imposes a suite of energetic constraints not measured in this study.

Colony area

A 1 ha increase in colony size resulted in a 9.4% increase in the odds of that colony avoiding extirpation (Figure 5.2 & Table 5.3). Individuals residing in larger colonies are more likely to be less vulnerable to predation, due to the benefits accrued from group-vigilance (Elgar 1989, Fairbanks & Dobson 2007) alarm calling (Carl 1971), and dilution (Bednekof & Lima 1998). For AGS, initial detection of an approaching predator typically precipitates rapid communication via alarm calls of this danger to all colony residents (Carl 1971). Individuals benefit from membership in a colony of larger extent because they receive these alarms further in advance of experiencing real danger than in a colony of lesser area. I cannot separate this proposed component of predation risk from the probable fact that larger colonies may also support larger populations which are buffered from random fluctuations in environmental and demographic factors (Lande 1993).

Visibility

Visibility as a factor determining predation risk is well established for small herbivores with similar life histories to AGS (Armitage 1982, Arenz & Leger 1997, Sharpe & Van Horne 1998, Bednekoff & Blumstein 2009, Ferrari, Bogliani & von Hardenberg 2009). In this study to perceive one additional 10cm² fraction of a 100cm² area at a distance of 50m increased the likelihood of colony persistence by 14% (Figure 5.2). Similar but less strong relationships were found at shorter distances (Figure 5.2). AGS rely heavily upon initial detection at extended distances to avoid predation (Carl 1971) and individuals that reside in more open habitats have higher survival than in closed areas because they detect predators from afar (Karels & Boonstra 1999). In addition to increased survival, Mateo (2007) found the Belding's ground squirrels decreased vigilance and increased foraging in areas with greater visibility. Given that overwinter

survival and subsequent spring breeding depends on the accumulation of body mass (fat and lean) before hibernation (McLean & Townes 1981, Sheriff et al. 2013a), the ability to increase feeding in areas of greater visibility may be of substantial importance. In a study of single burrow occupancy, Karels and Boonstra (1999) found that AGS burrows which remained in use, over several years of intensified predation, were in more open habitats containing fewer visual obstructions. In boreal forested habitats, visual occlusion has likely increased with the increase in above-ground biomass of understory shrubs (Grabowski 2015). Shrub expansion facilitated by warming climates serves as one possible explanation for the disappearance of AGS from forested habitats.

Interestingly, in ground dwelling sciurids, including AGS, it has been shown that increased visibility increases stress hormone levels (Blumstein et al. 2006, Mateo 2007, Sheriff et al. 2012), which may have long-term fitness consequences. Specifically, lower measured corticoids have been hypothesized to reflect a situation where predation risk at closed site is predictable. This may allow animals to mount large acute cortisol responses only when needed, thus facilitating escape from predators while also promoting glucose storage for the approaching hibernation (Mateo 2007).

Summary

Fine scale habitat characteristics believed to influence forage, predation risk, and overwinter survival jointly influence the spatial distribution of colony extinctions in this region. Evidence for multi-factor control of the distribution of this important northern herbivore within the southern portion of its range suggests that population responses to future environmental change will not be uniform. These findings add to a large body of work reinforcing the impact of both predators and bottom-up factors in the boreal forest and alpine tundra habitats (e.g., Hubbs

& Boonstra 1997, Karels et al. 2000, Hik et al. 2001, Donker & Krebs 2012). Whereas previous studies focused on a few populations in one habitat type, I provide the first large scale assessment of AGS populations for this region, and the largest survey of population status ever recorded for this species. Recolonization of unoccupied habitats by AGS is likely to be rare because dispersing squirrels preferentially settle near conspecifics (Boag & Murie 1981, Weddell 1991, Werner 2015) and because dispersal is male biased (Carl 1971, Byrom et al. 1999).

I raise two related questions for future research. Firstly, of the multiple mechanisms currently influencing AGS distribution, which factors play the greatest role and under which geographic conditions? Clarifying this question has the practical benefit of enabling us to predict the direction of population response to specific forms of environmental change. For example, with increasing summer temperature in northern regions, the strength of predation is predicted to increase due, in part, to the northward expansion of generalist predators (Callaghan et al. 2004). Climatic warming may therefore cause a shift from food to predator regulation in these northern systems (Legagneux et al. 2014). Such shifts should accentuate first at the southern limit of a herbivore species' range, where the strength of environmental harshness is least and the likelihood of novel interactions with more southern species is greatest (Callaghan et al. 2004). Secondly, do the relative strengths of these risk factors vary with latitude? Answers to both of these questions are best met through a combination of experimentation on a tractable scale, and studies which correlate population density with forage, predation risk, and burrow quality.

The fossorial behaviour of AGS, the permanency of burrows, and their tendency to live in discrete colonies presents an opportunity to quantify the causes and consequences of extinction and recolonization at large spatial scales. Arctic ground squirrels serve critically important roles within northern ecosystems as herbivores (McKendrick et al. 1980), prey item (Boonstra et al.

2001), and ecosystem engineers (Price 1971, Wheeler & Hik 2012); I propose that these qualities make them ideal candidates for studying and predicting the effects of environmental change.

Tables and Figures

Table 5.1: Explanatory variables used to in logistic regression analysis of colony occupancy and extinction of arctic ground squirrels of the Southwest Yukon, Canada. Supporting citations linking these parameters to survival and reproduction of fossorial rodents are provided below.

Parameter	Supporting Reference
Visibility % @ 5, 10, 15, 25, 50m	Hackett 1987, Sharpe & Van Horne 1998, Karels & Boonstra 1999, Van Vuren 2001, Sheriff et al. 2012.
Distance to shrub/tree cover continuous (0-100m) categorical (>100m)	Van Vuren 2001.
Slope 0-90°	Tomich 1962, Svendsen 1974, Weddell 1989, Blumstein et al. 2004, 2006.
Colony shape edge:area	Hackett 1987, Theberge & Wedeles 1989.
Soil depth continuous (0-120cm), categorical (>120cm)	Buck & Barnes 1999a, Armitage 2003, Ozgul et al. 2006.
Soil particle size % sand, silt, clay	Shaw 1926; <i>sensu</i> flood risk, Svendsen 1974, Weddell 1989, Greene et al. 2009.
Plant abundance % cover shrub, forb, grass, bare, total	Batzli & Sobaski 1980, Holmes 1984, Mclean 1985, Karels et al. 2000.
Plant diversity species richness (shrub, forb, grass, total)	Batzli & Sobaski 1980, Weddell 1989, Frank et al. 2009, Greene et al. 2009.
Elevation	Bronson 1979, Gillis et al. 2005.
Aspect mean, range	Armitage 2003, Werner et al. 2015a.
Incident solar radiation	Van Vuren & Armitage 1991.

Table 5.2: The top set of 10 component models selected for model averaging based on the cut-off criterion of being within 2 AIC_c units from the top model.

Component model	AIC_c	ΔAIC_c	Weight
1/4/5/6/9/10/14	49.37	0.00	0.17
1/4/6/9/10/14	49.48	0.11	0.16
1/2/4/6/9/10/14	50.03	0.67	0.12
1/4/6/9/10/11/14	50.48	1.11	0.10
1/3/4/6/9/10/14	50.49	1.13	0.09
6/10/11/13/14	50.69	1.32	0.09
1/4/6/8/9/10/14	50.83	1.46	0.08
1/4/6/7/9/10/14	51.14	1.78	0.07
1/4/6/9/10/14/15	51.16	1.79	0.07
1/4/6/9/10/12/14	51.23	1.87	0.07

(1)%bare (2)colony area (3)elevation (4)forb richness (5)Soil>120cm (6)%sand (7)%shrub cover (8)%silt (9)Slope angle (10)Soil depth 0-120cm (11)Viz@10m (12)Viz@15m (13)Viz@25m (14)Viz@50m (15)Viz@5m

Table 5.3: Model averaged parameter estimates and odds ratios predicting the occupancy status of arctic ground squirrel (*Urocitellus parryii*) colonies throughout the SW Yukon. Parameter selection is based on membership within 2 AIC_c units of the top ranked model. The predictors are continuous variables (except ‘soil depth>120cm’) whose estimates represent the log odds associated with a one-unit change in the predictor. The coefficients for a categorical predictor ‘soil depth>120cm’ represent the log odds of occupancy between that category and the reference category (soil depth<120cm). Relative importance was computed as the sum of the Akaike weights of the models which include that predictor.

Parameter	Estimate [*]	SE	Odds Ratio (95% CI)	Relative Importance
(Intercept)	-9.830	5.386	--	--
% Sand	9.293	5.124	1.097 (1.213, 0.993)**	1.00
Soil depth (cm)	9.146	3.715	1.096 (2.061, 0.581)**	1.00
Viz @ 50m	1.311	0.641	1.140 (1.293, 1.005)**	1.00
Slope angle (°)	1.214	0.683	1.129 (1.1291, 0.988)**	0.97
% cover bare	-0.706	0.387	0.932 (1.005, 0.864)**	0.91
Forb richness	5.759	3.333	1.059 (1.131, 0.922)**	0.91
Viz @ 10m	0.981	2.730	1.001 (1.065, 0.957)	0.18
Soil >120cm	0.487	1.379	1.627 (9.169, 0.041)**	0.17
Col_area (ha)	0.090	0.323	1.094 (2.061, 0.581)	0.12
Elev (m asl)	-0.177	0.739	1.000 (1.001, 0.998)**	0.09
Viz @ 25m	-0.092	0.326	0.991 (1.056, 0.930)	0.09
% Silt	0.090	0.453	1.009 (1.103, 0.923)	0.08
% cover shrub	-0.011	0.066	0.999 (1.012, 0.986)	0.07
Viz @ 5m	0.182	1.071	1.002 (1.023, 0.981)	0.07
Viz @ 15m	0.105	0.650	1.001 (1.014, 0.989)	0.07

^{*}Effect sizes have been standardized on two SD following Gelman (2008).

^{**}90% CI for these parameters do not include 1.

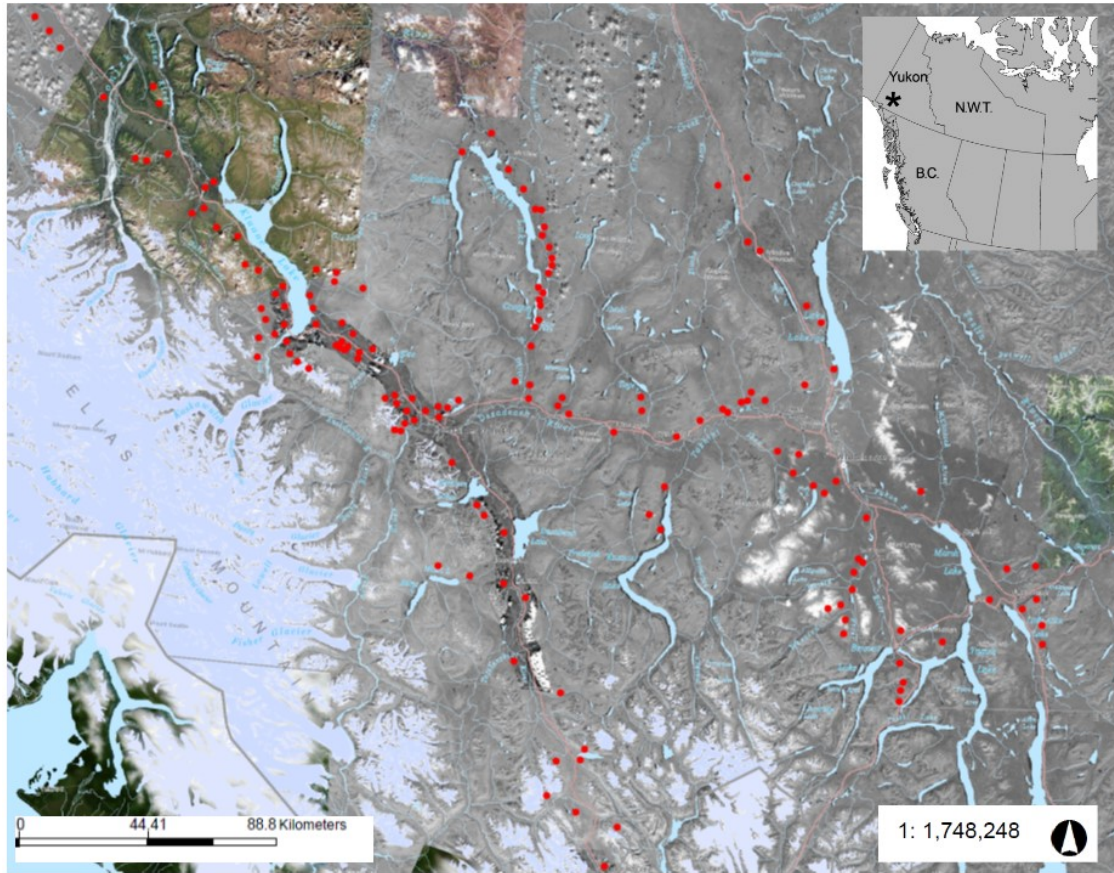


Figure 5.1 Red dots represent Arctic ground squirrel colonies sampled throughout a 25,000 km² area in SW Yukon and NW portions of BC, Canada from 2012 to 2014. The occupancy status of each colony was determined using an accurate powder-tracking technique at 138 sites.

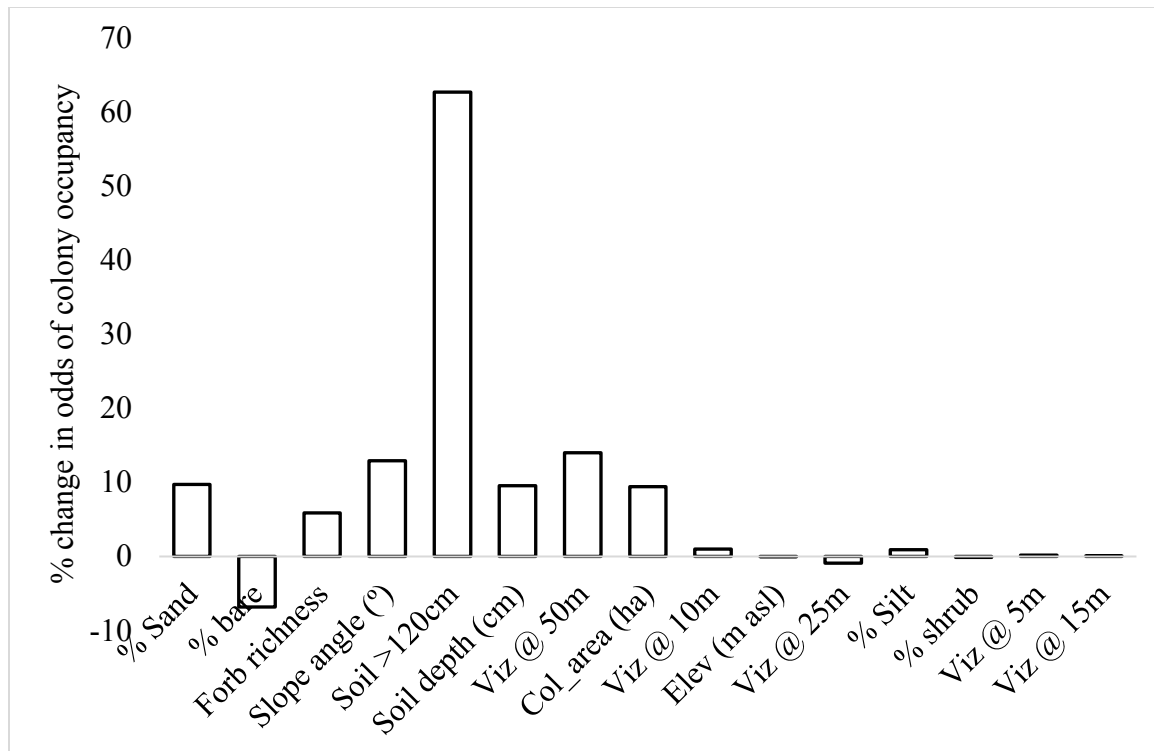


Figure 5.2 The percent change in the odds of occupancy with a single unit change of parameter.

These values are derived from the odds ratios in Table 5.3 [percent change = (odds ratio-1)*100].

Chapter 6: Conclusion

Thesis summary

In Chapter 2 I document the localised extinction of AGS in boreal forest after nearly three decades of continuous presence, as recorded from long term mark-recapture studies. Regional investigations reveal that the majority of populations in the forested valley bottoms have also been extirpated, but that nearby meadows retained some active colonies during that time. The source-sink relationship between meadow and forest habitats previously considered to maintain boreal forest populations has now broken down. Low active-season survival of forest-dwelling squirrels has contributed to population declines in these habitats.

In Chapter 3 I address one possible cause for the habitat-specific demography reported for two populations connected by dispersal. The body mass and condition of adult females from source (meadow) and sink (forested) habitats were compared during the early (May) and late (August) stages of the active season. Lower spring mass, accompanied by the achievement of increased mass gain prior to hibernation reveals a possible cause for lower spring reproductive rates and lower active season survival reported for forest-dwelling squirrels. However, by July 2016 most meadow populations in the Kluane region had also become locally extinct. The largest reductions in population sizes in both forest and meadows appear to be the consequence of low active-season survival associated with predator induced mortality.

In Chapter 4 I attempt to describe how predation caused the regular cyclic fluctuations in ground squirrel numbers and their extirpation from the boreal forest. Previous research has identified prey switching [from hares which are the dominant herbivore in this system to ground squirrels which are a secondary prey item], as the mechanism behind the AGS population cycles. Analyses of squirrel population growth rates at different phases of their cycle indicate that the

predator-prey relationship was inherently unstable because the predators continued to consume squirrels even as they became numerically rare. Patterns consistent with a Type II predator response reveal a single stable equilibrium and a lower density threshold—below which AGS numbers drift towards extinction. A strong correlation between historical hare abundance and squirrel abundance (coupled with past empirical research implicating predation in the oscillations of both species) is taken as evidence for indirect effects linking the two prey species. The loss of AGS - hare coupling after AGS numbers crossed below $\sim 0.5/\text{ha}$ is interpreted as further evidence of the unstable relationship between predators and secondary prey. In addition, an observed decline in the cyclic peaks of multiple hare cycles may indicate that regional predator density has increased over the past three decades. Some evidence for recent increases in regional predator density has been reported (Krebs et al. 2016).

In Chapter 5 I shift my attention away from the intensively studied populations of the Kluane region, towards the wider distribution of ground squirrels throughout Southern Yukon and Northern British Columbia. Here I describe food, soil and visibility characteristics associated with the persistence and/or extinction of ~ 150 arctic ground squirrel colonies throughout a $25,000 \text{ km}^2$ area. I make use of the burrowing behaviour of this species, and a unique method of indexing population density (Hubbs et al. 2000), to identify both extinct and extant populations with precision. Logistic regression models indicate that fine scale habitat characteristics associated with food, predation risk, and overwinter survival jointly influence the spatial distribution of colony extinctions in this region. These results suggest multi-factor control of the distribution of this important northern herbivore within the large southern portion of its range. Predicting the numerical response of arctic ground squirrels to environmental change will require

experiments designed to clarify in which habitats AGS populations are most sensitive to possible shifts to predation risk versus changes in the quantity and/or identity of available forage.

Wider implications

This dissertation essentially concerns how one meets the challenges inherent to what Graham Caughley (1994) coined the ‘declining population’ paradigm. Identifying the processes by which populations are driven to extinction by external forces continues to be a key challenge in ecological research. Notwithstanding the idiosyncrasies that frequently plague such endeavors, I make three observations which speak to the wider relevance of this research for ecologists and wildlife managers. First, those processes currently driving the altered population dynamics of AGS are likely to be implicated in wider patterns of ecosystem change. Large shifts in the regional distribution of this species are invariably a response to changing biotic and/or abiotic conditions common to other small mammals of north western Canada. Changes to the mechanisms responsible for both top-down and bottom-up population control have the potential to upset the trajectory of other medium body-sized prey.

Second, this research underscores the recent importance of predation for influencing the distribution and abundance of small herbivores in Canada’s north. Climatic warming of northern ecosystems is forecasted to intensify the role that predation may play in regulating small herbivores (Legagneux et al. 2014). If reductions in the mean abundance of snowshoe hares and ground squirrels from the boreal forest are not naturally reversed, the predator community in the montane boreal zone is likely to change significantly. However, predicting such changes will require knowledge of the complex numerical responses specific herbivore species are likely to

undergo in response to both environmental changes and modifications to the composition of predator communities (Sinclair & Krebs 2002).

Finally, because AGS were once so plentiful as to be responsible for approximately one-quarter of the energy flow at the herbivore level (Boonstra et al. 2001), their disappearance marks the non-trivial loss of tunnel building, food caching, and selective foraging known to affect local regimes of soil disturbance (Price 1971), nutrient cycling (McKendrick et al. 1980), plant diversity (Batzli & Sobaski 1980, McLean 1985), and trophic interactions (Wheeler & Hik 2012).

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Appendix A: Ongoing and future research

Whether arctic ground squirrels are undergoing permanent range of at low elevations, or whether this ‘low phase’ is to be followed by population recovery depends on whether the primary threatening processes that precipitated the decline have abated. My monitoring of large historical colony sites in Kluane ($n = 14$ colonies over six years, 2009 – 2015) indicates that recolonizations are likely infrequent (none recorded to date). Therefore, during 2013 – 2016 I experimentally reintroduced squirrels back into several large (~ 100 ha) historical meadow habitats. One of these meadows is situated on Kluane First Nation settlement land ($61^{\circ}23'21.35''$ N, $139^{\circ}6'13.86''$ W) and historically supported a sustainable traditional harvest (G. Pope, pers. comm. 2012). My purpose is to understand if and why habitat quality has been reduced to the point at which such meadows can no longer support viable populations. A portion of these translocated squirrels were fitted with radio collars (Holohil pd-2C units; $n = 105$) so that I could monitor their habitat use, minimum daily movement distances, and active season survival. Source populations were taken from the Burwash Landing airport ($61^{\circ}22'5.85''$ N, $139^{\circ}1'43.10''$ W).

As a means of increasing the strength of inferences to be drawn from this reintroduction project, one meadow was converted into a large (13 ha) choice experiment. I manipulated grass height and visibility (short grass and long grass treatments) and the number of available burrows. Treatment units were 50×50 m in size, oriented in a 5×10 pattern using a randomized block design. For the short grass treatment, vegetation height was reduced to 10 cm (range 0 – 23 cm) using gas-powered string trimmers. The tall grass treatment consisted of un-manipulated grassland with a mean height of 94 cm (range 15 – 114 cm). To alter burrow density, artificial burrows (50 cm deep and 7 cm in diameter) were dug using both gas- and hand-powered augers.

The low-density treatment was set to 50 burrows per hectare (approximately the number of natural burrows found in situ) and the high density treatment was increased to 200 burrows per hectare.

These data are still being analyzed. However, several themes have already emerged. First, active season survival of translocated individuals was generally low (0% – 50%), and nearly all mortalities (> 90%) were due to predation by coyotes or Red-tailed Hawks. A major complicating factor is that reintroductions often fail because translocated animals exhibit low site fidelity (Armstrong & Seddon 2008). My efforts were not unique in this respect: more than half of the ground squirrels moved out of the specified meadow and into surrounding forest. All of the dispersers from 2013 perished, prompting me in subsequent years to initiate soft release methods (e.g., the use of pre-release cages provisioned with food, water, and electric fencing; Figure A.1 & A.2) as a means of promoting site fidelity. In general, only those squirrels that settled in or near the experimental treatments survived their first summer.

Second, the use of larger release group sizes during 2014–2015 resulted in a corresponding shift from reintroduction failure to success (~50% annual survival). This result is consistent with the extinction thresholds predicted by predator-prey theory (Sinclair et al. 1998) and with the patterns previously observed in the monitoring data. Minimum group-size effects can be the result of social facilitation (i.e., Allee effects), as has been recorded for other rodent species (e.g., Barash 1989, Brashares, Werner & Sinclair 2010). Future experiments will be necessary to disentangle what mechanisms are responsible for these group-size effects.

Third, during post-reintroduction monitoring, unmarked ground squirrels from unknown sources were observed moving to and settling in the reintroduction area. Regular monitoring of five nearby control plots (to monitor immigration) indicated that areas farther from the

reintroduction site remained unoccupied despite the presence of adequate forage and burrow shelter. These findings point to the potential importance of patch occupancy and to the role that conspecific attraction (Smith and Peacock 1990) may play in the settlement decisions of dispersing squirrels. In keeping with these observations, Weddell (1991) reported that marked Columbian ground squirrels (*Urocitellus columbianus*) visit many suitable empty patches but settle only in occupied areas. A strong reliance on the use of conspecific cues for targeting high-quality habitat will impede population expansion via the recolonization of extinct patches. During July and August 2015, I formally tested the conspecific attraction hypothesis, using camera traps to monitor caged females placed in vacant meadows. The data will be analyzed during 2016-2017.

Tables and Figures



Figure A.1 Jeff Werner setting up soft-release nest boxes and electric fencing exclosures at the Duke River meadow reintroduction site (Kluane First Nation settlement land). (Photo: J. Werner)



Figure A.2 A caged yearling female with nest box in the Duke meadow. July 12 2015. (Photo: J. Werner)